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Changes in physiological traits associated with grain yield improvement in single-cross maize hybrids from 1930 to 1970

by

Diane Currie Tapper

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INTRODUCTION

The increased grain yields of maize (Zea mays L.) hybrids experienced by farmers over the past forty years have been due to the use of improved varieties grown with improved production practices, i.e., higher fertility, better weed control, increased plant densities, narrow row spacings, and improved crop management (Russell, 1974). Russell (1974) reported that, during the period 1922-1970, a total gain of 32.8 q/ha was realized by Iowa farmers. He calculated that 63.2% of this gain was due to genetically superior cultivars developed by breeding programs. In the past, plant breeders have achieved higher grain yields by direct selection for yield plus lodging and pest resistance (Russell, 1974; Duvick, 1977).

Plant breeders, however, are constantly seeking new procedures that will increase the efficiency of their breeding programs. Donald (1968) has proposed an alternate approach to yield improvement. He suggested selection for combinations of morphological and physiological traits to develop an optimum plant type, i.e., the crop ideotype. Mock and Pearce (1975) have described a maize ideotype for the theoretical optimum-yield environment. They described physiological and morphological attributes of a maize plant that would maximize light interception, partitioning of assimilate to the grain and sink strength and, theoretically, maximize grain yield.

If we may rationally expect higher yields from the development of the maize ideotype, conversely, we may ask what has been the physiological and morphological basis for higher grain yields achieved by maize breeders during the past forty years? As noted by Duncan et al. (1978), "...a better understanding of the differences among the cultivars and how these differences relate to their yield potentials should contribute to future yield improvement."

This question has been investigated in soybeans by Gay et al. (1980) and in peanuts by Duncan et al. (1978). Gay et al. (1980) compared various physiological attributes of a high-yielding cultivar with those of a low-yielding cultivar in each of two maturity groups. They found that yield increases in soybeans were associated with an increase in duration of the grain-filling period and partitioning of photosynthate to the seed. These physiological attributes were expressed as larger seed or more seed per unit area. Differences in yield potential among five peanut cultivars were due largely to the development of peanut cultivars that partitioned a larger proportion of their daily assimilate to the fruit (Duncan et al., 1978).

This study was an effort to determine possible morphological and physiological reasons for the increases in yield potential over the years reported by Russell (1974). Single-cross hybrids selected to represent the germplasm in use

during each decade from 1930 to 1970 were grown at three plant densities in a split plot design:

1. To evaluate changes in machine-harvestable and total grain yield potential across decades of maize breeding.
2. To study the relationship between morphological and physiological changes in the maize plant as a source of assimilate and grain yield potential.
3. To examine the relationship between morphological and physiological changes in the maize ear-sink and grain yield potential.
4. To determine the relationship between physiological changes in the partitioning of assimilate from the source to the sink in the maize plant and grain yield potential.
5. To compare physiologically and morphologically the performance of decades of hybrids at low, medium, and high plant densities.

REVIEW OF LITERATURE

Grain Yield Improvement: The Contribution of Plant Breeding

Beginning with the introduction of hybrids during the 1930s and continuing through the 1970s, maize producers have enjoyed substantial improvements in grain yields. These improvements in maize grain yields have been due to improved production practices along with the use of genetically superior hybrids. Russell (1974) compared maize hybrids representing all eras of plant breeding since the 1930s under modern high production management. He reported that 63.2% of the increase in maize grain yield in Iowa during the period 1922-1970 could be attributed to the use of genetically improved hybrids. In a similar experiment, which employed different genotypes representing the 1939-1971 period, Duvick (1977) concluded that 57% of total grain increases were due to maize breeding efforts. The calculated rates of genetic gain for these studies were 0.62 q/ha/yr (Russell, 1974) and 0.50 q/ha/yr (Duvick, 1977). The higher rate of gain for the study by Russell (1974) may be due to the fact that it was calculated over a time period which included the important increase in yield potential associated with the change from open-pollinated varieties to maize hybrids. Traditionally, the major emphasis of maize breeding programs has been selection for higher grain yields in association with

lodging resistance and ear retention.

In addition to increased grain yield potential, Russell (1974) and Duvick (1977) found substantial reductions over the years for stalk and root lodging with little change in the number of dropped ears or barrenness. The importance of high plant densities for the expression of yield potential of more recent hybrids was apparent in both studies. Duvick (1977) found little change in yield at a low plant density. Likewise, at a low plant density, Russell (1974) found only the mean yield of the most recent group of hybrids to be significantly higher than the mean yields of earlier groups of hybrids, which were not significantly different from one another.

Grain Yield Improvement: A Physiological and Morphological Basis

Grain yield is the expression of a large number of physiological processes and morphological traits. Observed improvements in the genetic grain yield potential over the years may logically be assumed to be associated with alterations of these basic processes and traits. Duncan et al. (1978) pointed out that a knowledge of the physiological and morphological basis of grain yield improvements should be of practical value in future plant breeding efforts.

Physiological traits of four peanut cultivars representing 40 years of breeding were examined by Duncan et al. (1978) in an effort to detect changes responsible for the increase

in yield potential. They reported that increases in yield potential appeared to be related to increases in (1) the proportion of assimilate partitioned to reproductive organs, (2) the length of the fruit filling period, and (3) the rate of fruit establishment. Assimilate partitioning appeared to be the primary determinant of fruit yield.

Similarly, Gay et al. (1980) sought an understanding of the physiological basis for yield potential differences between two soybean cultivars in each of two maturity groups. Yield potential differences between the two cultivars representing Maturity Group III were associated with the duration of the seed filling period. In Maturity Group IV, however, observed differences in yield potential were related to a larger proportion of the plant photosynthate being partitioned to a larger number of seeds.

Various populations of maize have been subjected to recurrent selection for grain yield for long periods of time. The value of recurrent selection for the improvement of grain yield has been established (Hallauer, 1981). The existence of unimproved populations of maize and improved cycles of selection derived from those populations presents an opportunity to compare physiological and morphological traits associated with different yield potentials. Fakorede and Mock (1978) evaluated population crosses between unimproved (C0) and improved (C7) populations of BSSS(R) and BSCB1(R).

Grain yield improvements shown by improved population crosses were associated primarily with increased sink size achieved through longer grain-filling duration and increased partitioning of assimilate to the grain. Similar evaluations of unimproved and improved populations of BS12 were made using B14 as a tester. The larger grain yield of the improved BS12 population also was associated with increased partitioning of assimilate to the grain. Crosbie and Mock (1980, 1981) also evaluated and compared physiological and morphological traits in crosses and testcrosses of maize populations which were improved by means of recurrent selection. In general, they found observable grain yield improvements to be associated with increases in ear-sink size (Crosbie and Mock, 1980). The physiological bases for these increases in ear-sink size, however, were peculiar to the maize population (Crosbie and Mock, 1981).

What practical value can be foreseen for an understanding of the physiological and morphological basis of maize grain yield improvement? Donald (1968) has suggested, as an alternative to breeding programs based on selection for yield, a long-term breeding program designed to develop a model plant, i.e., ideotype, for a defined environment. An ideotype of maize adapted to high production environments has been described by Mock and Pearce (1975). Their ideotype of maize would be characterized by efficient use of solar

radiation, maximum partitioning of the photosynthate to the grain, adequate sink strength, small tassels, a short pollen-shed-to-silking interval, cold tolerance, and photoperiod insensitivity. The feasibility of ideotype development, however, is based on the existence of genetic associations between grain yield and the traits characterizing the ideotype. Hence, it would appear that investigations of the physiological and morphological basis for maize grain yield improvement may provide the information needed for the development of maize ideotypes. Crosbie and Mock (1980) have suggested that identification of traits limiting grain yield in maize populations may allow yield-component modification schemes to improve grain yield.

Grain Yield: Its Relationship to Plant and Ear Heights

The effect of plant and ear heights _per se_ and their relationship to one another on grain yield is not known. El-Lakany and Russell (1971) found plant and ear height to be significantly correlated with grain yield at low, medium, and high plant densities. The range of these correlation coefficients was 0.44 to 0.56. Hallauer (1971), however, found no correlative response of plant and ear height with reciprocal recurrent selection for yield in Stiff Stalk Synthetic and Corn Borer Synthetic No. 1. Crosbie et al. (1978b) indicated

that, while plant and ear heights were correlated with dry matter per plant in the Iowa Stiff Stalk Synthetic maize population, correlations between plant and ear heights and grain yield or grain per plant were not significant. Evaluation of a synthetic population developed by selection for lower ear height by Vera and Crane (1970) revealed a significant change in ear height, but no significant differences in yield, grain moisture, or lodging. In a subpopulation selected for lower ear height, Acosta and Crane (1972) found grain yield to be reduced. These studies reveal little about the relationship of plant and ear height to yield. More recently, Moll et al. (1975) have stated that the genetic association between yield and ear height is not linear. They suggested instead that an optimum ear height might exist for maximum yield. They speculated that, if the ear is positioned low on the stalk, leaves above and proximal to the ear may be shaded, thus reducing grain yield. Ears positioned high on the stalk, however, may have too few leaves above them, which also may reduce grain yield.

Harville et al. (1978) suggested that selection programs utilizing additive gene effects should effectively change ear height means. Analysis of the genetic basis of ear height in two inbred lines of corn led Giesbrecht (1961) to conclude that six genetic factors could explain observed differences. He reported a high heritability of 82.4% for ear height.

Unlike a previous study (Acosta and Crane, 1972), Josephson and Kincer (1977) and Harville et al. (1978) found that manipulation of ear heights involved not only variation in internode length but also placement of the ear on the stalk. They also indicated that ear heights may be reduced without reducing plant height. Thus, manipulation of ear placement on the stalk and its resulting effect on leaf canopy above the ear may suggest an association between ear height and grain yield (Moll et al., 1975).

Grain Yield: The Product of Biological Yield and Harvest Index

Until a fuller understanding of the complex growth and development processes in plants is available, Donald and Hamblin (1976) recommended studying biological yield and harvest index because they employ relatively simple techniques yet provide a more complex analysis of grain yield. Total grain yield is the product of biological yield and harvest index. Therefore, one would expect high correlations between grain yield and its two components, biological yield and harvest index. The actual relationship between higher grain yield and harvest index in maize has not been widely investigated. Fakorede (1977) and Fakorede and Mock (1978) have found that variety hybrids of improved populations of BSSS(R), BSCB1(R), and BS12 displayed significantly higher

harvest indices than variety hybrids of the corresponding unimproved populations. Their data did indicate significantly higher yields in hybrid varieties formed from improved populations. Crosbie and Mock (1981) also evaluated unimproved and improved populations of the BSSS(R) and BSCB1 by means of both population crosses and testcrosses. Crosses involving all improved populations displayed a significantly higher grain yield than crosses of the unimproved populations. The increased grain yield per plant of the improved population of BSSS(R) was the result of significantly higher harvest index as dry matter per plant did not increase. Both increased dry matter per plant and harvest index contributed to higher grain yield in testcrosses of improved BSCB1(R). Higher grain yields of the population crosses, however, were associated with higher dry matter per plant. Crosbie et al. (1978b) evaluated 64 random inbred lines from BSSS and reported a highly significant correlation between dry matter yield and grain yield. In a study to determine a useful means of selecting hybrids for the production of maize silage, Genter and Camper (1973) observed that, in general, high grain yields were associated with high dry matter production. Thus, it appears that increased grain yields may be due to the increase of either or both biological yield and harvest index.

Grain Yield: The Product of Rate and Duration of Grain Filling

Higher grain yields are the expression of more dry matter being partitioned to the grain. The amount of dry matter partitioned to the grain is the product of rate of grain filling and duration of the grain-filling period. The close association implied between the grain-filling duration and grain yield has been substantiated by several studies (Hanway and Russell, 1969; Daynard et al., 1971; Cross, 1975; Fakorede and Mock, 1978; Crosbie and Mock, 1981). Hanway and Russell (1969) calculated the number of days after silking required to produce observed grain yields. A range of 17 days in grain-filling duration among the 11 maize hybrids indicated considerable variation. They also noted an association between grain-filling duration and final grain yields when hybrids were grown and compared in similar environments. Daynard et al. (1971) were the first to calculate the duration of that part of the grain-filling period when the rate of grain filling is linear, i.e., the effective filling period duration. They found a significant linear relationship between grain yield and effective filling period duration. Both Fakorede and Mock (1978) and Crosbie and Mock (1981) reported that increased grain yields resulting from recurrent selection in BSSS(R) and BSCB1(R) were related to longer grain-filling duration. The high phenotypic

correlation, i.e., r = 0.81**, reported by Cross (1975), corroborates the relationship between grain yield and grain-filling duration. Numerous reports of genotypic differences in grain-filling duration (Hillson and Penny, 1965; Hanway and Russell, 1969; Daynard and Duncan, 1969; Daynard et al., 1971; Daynard, 1972; Carter and Poneleit, 1973; Cross, 1975; Fakorede and Mock, 1978; Crosbie and Mock, 1981) along with the large general combining ability effects for grain-filling duration reported by Cross (1975) suggest that genetic extension of the grain-filling duration is feasible.

However logical a close relationship between rate of grain filling and grain yield appears, a review of the literature does not reveal a convincing amount of evidence to substantiate this relationship. Daynard et al. (1971) reported that less than 16% of the differences in grain yield of several maize hybrids were explained by differences in rate of grain filling. In a diallel analysis of seven inbred lines of maize, Cross (1975) found the correlation between rate of grain filling and grain yield to be nonsignificant. Crosbie and Mock (1981), however, found that rate of grain filling was significantly higher in populations of BSSS(R) and BSCB1(R) which had been improved for grain yield. Although Hanway and Russell (1969) found little difference in rates of grain filling among selected hybrids, several recent reports indicated that genetic differences for rate of grain

filling exist (Daynard et al., 1971; Johnson and Tanner, 1972; Carter and Poneleit, 1973; Cross, 1975; Crosbie and Mock, 1981). These genetic differences suggest a potential for selection to alter the rate of grain filling.

Biological Yield: The Product of Photosynthetic Rate, Leaf Area, and Duration

Photosynthesis is basic to the production of dry matter and thus presumably directly related to yield. Mock and Pearce (1975) cite maximum photosynthetic efficiency as an integral part of their maize ideotype. The total amount of dry matter produced by a maize plant during the growing season depends upon three aspects of the photosynthetic process. First, factors limiting the rate of photosynthesis determine the amount of CO_2 fixed per unit area per unit of time given defined environmental conditions. Photosynthetic efficiency has most often been estimated by determining the carbon dioxide exchange rate (CER) of a leaf or plant canopy. Second, the amount of photosynthetically active leaf area is a determinant of total dry matter produced by the plant. This is a function of both the total leaf area per plant and the canopy architecture which determines distribution of solar energy over the leaf surfaces. Finally, the amount of time during which the plant is photosynthetically active will affect the total amount of dry matter produced over the growing season. Recognition of the physiological and morpho-

logical factors important to dry matter and grain production has led researchers to study the relationship of these factors to grain yield.

Positive correlations between leaf and canopy CO_2 exchange rates and dry matter production in maize have not been found in experimental work. Single crosses derived from a range of high to low photosynthetic lines displayed significantly different CERs, biological yields, and grain yields, but neither grain nor biological yield was positively correlated with leaf CERs of the single crosses or the parental strains (Musgrave, 1971). Sixty-four maize inbred lines, randomly derived from BSSS, were evaluated for CER, morphological traits and yield traits by Crosbie et al. (1978b). They reported no genetic or phenotypic correlations between leaf CER and either dry matter yield or grain yield. They pointed out, however, that while selection for increased CER would not increase grain yield in BSSS, removal of sink limitations through selection might improve the correlation between CER and yield. This is a good example of the type of biological interaction which must be considered when looking for factors contributing to high grain yield. Fakorede and Mock (1978), likewise, found no relationship between CER and higher yield in four variety hybrids of maize populations improved through recurrent selection. Moss and Musgrave (1971) reported no positive correlations of leaf CER with

canopy CER or yield. Considering the number of factors, i.e., plant height, leaf angle, leaf area, and maturity, in addition to leaf CER influencing canopy CER, the absence of positive correlations is perhaps not surprising.

Expectation of a positive correlation of leaf CER with grain yield may be a rather simplistic approach. It would seem realistic, however, that canopy CER would be correlated with at least dry matter production. Lake (1972) and Leafe (1972) reported some evidence that this assumption may be correct for several species. Vietor and Musgrave (1979) combined data from leaf canopy CERs and climatic conditions and estimated a cumulative carbon dioxide exchange during the grain-filling period for two maize hybrids derived from photosynthetically selected high and low lines. They found that cumulative carbon dioxide exchange would not adequately account for total above ground weight change during the grain-filling period.

Although evidence for a strong relationship between CERs and dry matter production is limited, Mock and Pearce (1975) suggested that their maize ideotype should possess the biochemical and morphological potential to maximize utilization of solar energy in the production of dry matter. The variability of CER required by plant breeders for selection has been demonstrated (Duncan and Hesketh, 1968; Heichel and Musgrave, 1969; Fousova and Avratovscukova, 1967; Crosbie

et al., 1977, 1981). Duncan and Hesketh (1968) reported a range of 36 to 59 mg CO_2 dm^{-2} leaf area h^{-1} at 30°C in CERs among 22 races of maize. The range of CERs determined by Crosbie et al. (1977) among 64 random inbred lines from the Iowa Stiff Stalk Synthetic (BSSS) was similar to the range of 21 ± 2 to 59 ± 3 mg CO_2 $dm^{-2}h^{-1}$ reported by Heichel and Musgrave (1969) for seven maize inbreds grown in a temperate region. Genotypic differences for CER among the 64 random inbred lines were highly significant and narrow-sense heritability estimates were 0.58 and 0.80 for the vegetative and grain-filling growth stages, respectively. The nature of the genetic variance was further elucidated by Crosbie et al. (1978a). They found that CER differences among four low and four high CER inbreds were controlled largely by additive effects. These results indicated that selection among inbred lines of maize would be effective and they were confirmed by Crosbie et al. (1981). They reported actual selection advance among inbred lines of 4.7 and 5.7% for CER during vegetative and grain-filling growth stages, respectively.

In addition to high leaf photosynthetic rates, Mock and Pearce (1975) pointed out that efficient utilization of solar radiation is achieved only when a major portion of the incipient solar radiation is intercepted and distributed over maximum leaf area. Light interception and distribution by the plant is determined by leaf area index, the distribution

and size of leaves within the canopy, leaf orientation, and interception of light by nonphotosynthesizing parts (Mock and Pearce, 1975).

More effective light interception may be achieved by increasing leaf area per plant or more simply by using high plant densities and narrow-row spacings. Mock (1977) suggested that a maize crop should intercept at least 95% of the solar energy available and this would be achieved if maize hybrids were grown at plant densities greater than 80,000 plants/ha. With greater amounts of solar radiation being intercepted, increases in dry matter production and grain yields might logically be expected. Manipulation of total light interception by varying plant densities and row spacing to give different leaf area indices has allowed testing of this concept. In general, grain yield and leaf area index have been found to be linearly related at leaf area indices up to 4.0 (Hoyt and Bradfield, 1962; Eik and Hanway, 1966; Williams et al., 1968; Rutger et al., 1971; Scarsbrook and Doss, 1973; Johnson, 1973). At higher leaf area indices, grain yield did not increase as quickly as did leaf area index. Johnson (1974) pointed out that the distribution of leaf area index within the canopy has an effect on grain yield apart from the effect of total leaf area index. He suggested that leaf area above the ear exerts its effect on yield through weight per kernel and kernels per row, while the leaf

area below the ear exerts its effect on yield through kernels per row only. Optimum leaf area indices for specific genotypes, therefore, may be determined and achieved with proper plant densities and row spacings. Use of high plant densities to achieve high light interception requires the use of density-tolerant genotypes. Less density-tolerant genotypes may have optimum leaf area indices which do not maximize light interception.

In order for maximum leaf area to be exposed to the intercepted solar energy, leaf orientations must allow light to penetrate into the canopy. Mock and Pearce (1975) pointed out that maize plants photosynthesize more efficiently at lower light intensity. For example, at 50% full sunlight, maize achieves 80% of maximum photosynthesis. The importance of distributing the solar energy over more leaf area is obvious. The important contribution of photosynthate by all leaves above the ear to the grain during grain filling (Eastin, 1969; Fairey and Daynard, 1978) necessitates the penetration of sunlight at least to the ear leaf. Williams et al. (1968) commented, however, that leaf area indices greater than 4.0 substantially reduce light penetration in normal canopies. Therefore, the use of high plant densities to achieve maximum interception of solar radiation establishes the need for a leaf orientation that will allow light penetration into the lower canopy.

Analyses of mathematical models simulating photosynthesis in crop stands (Duncan et al., 1967; Loomis and Williams, 1969; Duncan, 1971) indicated that distribution of solar radiation over more total leaf area would be enhanced in plants possessing erect leaves above the ear and intermediate to horizontal leaf orientation below the ear. More efficient use of solar energy might be expected to increase dry matter production, which may be diverted to the grain for increased grain yield. The utility of this type of canopy has been tested in field trials with mixed results. Pendleton et al. (1968) found a 40% grain yield increase for liguleless Hy x C103 as compared with normal Hy x C103. They also reported that mechanical manipulation of the leaves of Pioneer 3306 to produce an erect leaf canopy resulted in grain yield increases of 14%. Winter and Ohlrogge (1973) reported that LAIs of 4.3-4.7 were required for cultivars with upright leaves to produce higher yields than did the check at its optimum population. Lambert and Johnson (1978) also found that liguleless-2 hybrids produced 6.7 and 12.9% more grain only at plant densities of 75,000 and 90,000 plants/ha, respectively, than did hybrids with normal leaf type. While Pepper et al. (1977) also reported grain yields of a group of three erect-canopy inbreds to be significantly higher than inbreds with horizontal canopies only at very high plant densities, i.e., 160,000 plants/ha, Mock (1977) found that the

relationship of leaf canopies and grain yield for a group of hybrids was obscure at this plant density because of extreme barrenness. Similar studies (Ariyanayagam et al., 1974; Whigham and Woolley, 1974; Hicks and Stucker, 1972; Russell, 1972, Mason and Zuber, 1976), however, did not find leaf angle to be a significant yield determining trait. In a more recent study of the Iowa Stiff Stalk Synthetic maize population, Crosbie et al. (1978b) found leaf area per plant, leaf orientation above and below the ear, and leaf area index to be phenotypically correlated with dry matter yield and dry matter per plant, without being correlated to grain yield or grain per plant. Evaluation of variety hybrids of the unimproved and improved cycles of BSSS(R) and BSCB1(R) indicated that crosses of improved cycles exhibited higher grain yields in association with increased erectness of the leaf canopy. Mock and Pearce (1975) pointed out that leaf orientation is only one of many factors determining grain yield and, in order for it to exert a positive effect on yield, other factors cannot be limiting. On this basis, they have included erect leaf orientation as part of their maize ideotype.

Successful selection for change in leaf orientation, i.e., 10 to 12% per cycle, has been reported by Ariyanayagam et al. (1974). Heritability estimates of 69-80% for canopy orientation above the ear and 65-78% for canopy orientation below the ear are reported by Mock (1977) and suggest that

sufficient genetic variability exists to successfully alter canopy orientation by selection.

A third dimension of total photosynthate production is duration of the photosynthetic period. Maximization of photosynthate production during grain filling is critical because approximately 80% of the photosynthate produced by maize plants during grain filling is diverted to the ear-sink (Eastin, 1969). Mock (1977) pointed out that availability of solar energy over the growing season is not uniform and that grain filling normally occurs during a low-solar energy period. Photosynthetic rates in maize increase with increased light intensity (Mock and Pearce, 1975); thus, it should be valuable to have the grain-filling period coincide with that period of maximum solar radiation. Mock and Pearce (1975) and Mock (1977) suggested that earlier planting dates could be a means to achieve earlier flowering and coincidence of grain filling and maximum solar radiation. They acknowledge the need for maize genotypes whose germination and early growth processes are cold tolerant because early planting dates result in much lower soil and air temperatures after planting.

Any cultural practice or physiological process resulting in earlier establishment of autotrophic maize seedlings should increase dry matter production potential by increasing the photosynthetic duration of the life cycle of the plant if

date of senescence does not change and by allowing grain filling to begin earlier during periods of greater solar radiation. Hanson (1971) reported results of a divergent selection scheme for differential productivity in juvenile maize plants. His data indicated that high dry matter production injuvenile maize plants was associated primarily with 30% greater leaf area. Maize breeders recently have included a spring vigor rating, which is a visual comparison of total green tissue area in a stand of juvenile plants, in their evaluation programs. Glenn et al. (1974), however, found little relationship between any measure of spring vigor in single crosses of parents with diverse seedling vigor and grain yield.

An increase in the amount of photosynthate produced during the grain-filling period may also be envisioned by combining an increase in the duration of the grain-filling period with an increase in the duration of the photosynthetic period as a result of delayed leaf senescence. Growth analyses have demonstrated an association between increased dry matter production and delay of leaf senescence in certain varieties of maize (van Eijnatten, 1963; Adelana and Milbourn, 1972). Duvick (1977) found increased grain yields over 40 years of maize breeding to be associated with important improvements in resistance to premature death. Certain populations of maize, improved through recurrent selection for yield, also

displayed a lengthened stay-green period (Fakorede, 1977; Crosbie and Mock, 1981).

Grain Yield: Its Relationship to Ear-Sink Strength

King et al. (1967) and Bingham (1967) have discussed the function of sink strength, as determined by grain size and number, on the determination of grain yield. Results of their study led Tanaka and Yamaguchi (1972) to conclude that sink size, determined by number of kernels per unit field area, was the limitation to increased grain yields. Based on these assertions, one would expect to find reports of significant correlations between sink strength and grain yield. El-Lakany and Russell (1971) evaluated various traits in crosses of 20 F_5 lines divided into two groups on the basis of their ability to produce grain with increasing plant density. Their data indicated significant correlations between number of ears per plant, ear length, kernel depth, and number of kernels per plant with grain yield at high plant density. They concluded that number of ears per plant was the single most important determinant of yield differences between the density-tolerant and density-intolerant groups. Russell et al. (1973) also found the number of ears per 100 plants to have increased in two maize populations in association with recurrent selection for specific combining ability for grain yield. Obilana and Hallauer (1974) reported genetic correlation coefficients of

0.76 for kernel depth with grain yield and 0.58 for ear length with grain yield. This correlation of kernel depth with grain yield also was reported by Hallauer (1971) in BSSS and BSCB1. Walejko and Russell (1977) reported, however, no consistent changes in ear traits with changes in yield. Similarly, Fakorede and Mock (1978) evaluated several grain yield components and found only kernel weight to have significantly increased in BSSS(R) x BSCB1(R) as a result of recurrent selection for grain yield. Evaluation of 64 random inbred lines from BSSS revealed significant correlations of ear length, ear diameter, ears per plant, and kernel weight with grain yield (Crosbie et al., 1978b). They concluded that an adequate receptive ear-sink was an important limitation to grain yield in BSSS. Crosbie and Mock (1980) reported that improvements in grain yield were associated with increases in ear-sink size. Increases in ear-sink size were manifested by different means in different populations. Crosbie and Mock (1980) suggested the need to identify traits limiting grain yield in maize populations prior to attempting grain increases through yield component modifications.

Adequate genetic variation in ear traits for selection seems to exist in most populations (Hallauer, 1971; Obilana and Hallauer, 1974). Heritabilities, on a mean basis, for ear length and kernel depth of 76.6 and 65.3%, respectively, were reported by Obilana and Hallauer (1974).

In order to maximize interception of solar radiation, maize must be grown at high plant densities (Mock, 1977). At high plant densities, however, efficient conversion of intercepted solar radiation to grain is limited by barrenness (Stinson and Moss, 1960; Woolley et al., 1962; Buren et al., 1974). Buren et al. (1974) reported correlation coefficients between grain yield and barrenness at 98,800 plants/ha of -0.89, -0.89, and -0.76 for three different experiments. El-Lakany and Russell (1971) designed an experiment to determine the effect of increasing plant density on density-tolerant versus density-intolerant maize lines. They found that high plant densities exaggerated the pollen-shed-to-silking interval in all lines but to a lesser extent in the density-tolerant lines. This effect of high plant densities on the pollen-shed-to-silking interval has also been noted by Woolley et al. (1962). Study of the morphological and physiological basis of tolerance to high plant density led Buren et al. (1974) to report that density-tolerant genotypes were characterized by a short silking interval, a short pollen-shed-to-silking interval, rapid growth of the first ear, prolificacy, reduced tassel size, and more efficient production of grain per unit leaf area. In general, these observations were confirmed by Smith et al. (1982). Heritability estimates for these traits in the BSUL1 maize population were all relatively high with the exception of grain per

unit leaf area. Smith (1977) reported predicted gains from selection for various traits associated with barrenness and grain yield. Predicted gains indicated that selection for any of these traits may be expected to increase yields and reduce barrenness at high plant densities.

My review of the literature has revealed that most traits, which we expect to contribute to grain yield, have been shown to be associated with grain yield in some studies while the same trait may also have been shown not to be associated with grain yield in other studies. Perhaps this is not surprising considering that most experiments employed different genetic materials. The limitation to grain yield in different gene pools would not be expected to be the same. Reported data indicated that, in general, these traits may be selected successfully to develop a model maize plant or to selectively upgrade maize populations. Any of these traits may have been indirectly altered as a result of selection for higher maize grain yield during the past 40 years and thus provided a basis for observed increases in grain yield (Russell, 1974; Duvick, 1977).

MATERIALS AND METHODS

Plant Materials

The plant materials used in the following experiments included 20 open-pedigree single-cross hybrids and four private company hybrids, hereinafter referred to as public and proprietary hybrids, respectively. Four public single-cross hybrids were selected to represent the germplasm in use during each decade from 1930 to 1970 (Table 1). Although double-cross hybrids were more commonly used until the 1960s, single-cross hybrids used were the nonparental single-cross hybrids forming those double-cross hybrids. Nonparental single-cross hybrids are the genotypes in a double-cross hybrid resulting from the cross of two single-cross hybrids. The double-cross hybrids represented by the single-cross hybrids used in this study (Table 1) are given in Table 2 along with their first year of production. Single-cross hybrids were used instead of double-cross hybrids for two reasons. First, comparisons of traits across decades would not be confounded by use of genetically different types of plant materials. Secondly, the homogeneity of the single cross was desirable to reduce sampling problems. All hybrids selected were of approximately the same maturity. These single-cross hybrids were AES 700 maturity. Four private companies were asked to provide seed of their best hybrid of

Table 1. Public hybrids selected to represent the germplasm in use during each decade from 1930 to 1970

Decade	Hybrid	Decade	Hybrid
1930	Os420 x L289	1960	B14A x B54
	Os420 x I205		B37 x B54
	L289 x I205		Oh43 x B37
	Os426 x C1447		Oh43 x B14A
1940	Wf9 x Os420	1970	B73 x Mo17
	M14 x 187-2		B73 x B70
	I205 x 187-2		B37 x B70
	M14 x L289		A632 x Mo17
1950	B14A x Wf9		
	M14 x B14A		
	187-2 x B14A		
	Wf9 x 187-2		

AES 700 maturity, provided that they did not duplicate any of the open-pedigree single crosses. These proprietary hybrids included Pioneer 3541, Northrup King PX37, DeKalb XL55A, and Funks G4520.

In 1979 and 1980, seed of the parent inbred lines used in the public hybrids were removed from cold storage and appropriate crosses were made in paired rows. All rows of each pair were harvested and reciprocals were bulked to provide an adequate amount of hybrid seed. Seed for the hybrids was generated in the year prior to its use in the experiments to be described. Private company seed was donated the spring of 1980. This seed was placed in cold storage and used in both the 1980 and 1981 seasons.

Table 2. Double-cross hybrids used by Russell (1974) to represent each decade from 1930 to 1960

Hybrid no.	Group no.	Pedigree	First year of production for experimental purposes
Ia 942	1	(Os420xOs426)(L289xI234)	1929
Ia 939		(Os420xOs426)(L289xI205)	1929
Ia 306		(L289xI205)(Wf9xOs420)	1939
Ia 931		(Os420xOs426)(L289xC1447)	1929
Ia 4249	2	(Wf9xOs420)(187-2xM14)	1940
Ia 4297		(Wf9xI205)(187-2xM14)	1940
Ia 4298		(Wf9xM14)(Os420x187-2)	1940
Ia 4316		(Wf9xM14)(I205xL289)	1941
Ia 4570	3	(Wf9xB14A)(187-2xM14)	1950
Ia 4575		(Wf9xB14A)(Os420xM14)	1950
Ia 4599		(Wf9xM14)(B14Ax187-2)	1951
Ia 4600		(Wf9xM14)(B14AxOs420)	1951
Ia 5369	4	(Wf9xB14A)(B37xB54)	1960
Ia 5371		(Wf9xB14A)(B54xN22A)	1960
AES704		(Wf9xOh43)(B14AxB37)	1955

[a]Adapted from Russell (1974).

Experimental Procedures

In 1980 and 1981, the plant materials were evaluated at the Agronomy and Agricultural Engineering Research Center near Ames, Iowa and the Ankeny Research Center at Ankeny, Iowa. Three replications of a split-plot design were used. Plant densities were main plots and hybrids were subplots. Numerical specifications of low, medium, and high plant densities at each environment are given in Table 3. Subplots consisted of four rows 5.49 m long spaced 76 cm. All subplots were overplanted and subsequently thinned to the desired plant density. Uniformity of cultural practices was sought across all experiments. A preplant application of herbicide, cultivation, and hand-weeding provided weed control. Fertilizer applications included approximately 170 kg N/ha (preplant application) and 90 kg P and K/ha. The four environments provided diverse growing conditions. During both years, experiments at Ames suffered from prolonged dry periods during July and August. Subsoil moisture was more limiting to corn growth in 1981 than it was in 1980. Growing conditions were very favorable, however, at Ankeny in 1981.

Seedling emergence and vigor

Five weeks following planting, the number of plants in the left-border row of each subplot was counted and

Table 3. Terms used to describe plant densities used in four environments

Plant density	Environments			
	Ames 1980	Ankeny 1980	Ames 1981	Ankeny 1981
	1000 plants/ha			
Low (L)	29.3	31.7	29.3	29.3
Medium (M)	43.9	51.2	43.9	43.9
High (H)	58.5	63.4	58.5	58.5

percentage emergence was calculated.

In order to compare seedling vigor of these hybrids, the center two rows of each subplot were rated visually for amount of green leaf area displayed at an early vegetative stage, i.e., 45 days after planting at Ames and Ankeny in 1980 and 35 and 42 days after planting at Ames and Ankeny, respectively, in 1981. A 1 to 9 rating scale was used. A rating of 1 indicated the least amount of green leaf area and 9 indicated the greatest amount of green leaf area. Visual ratings considered both plant height and leaf area.

Carbon dioxide exchange rate

Carbon dioxide exchange rate (CER) measurements were made each year only at the Agronomy and Agricultural Engineering Research Center at Ames, Iowa. A method for measurement of CER on excised leaves as described by Pearce et al. (1976)

was followed. In 1980, CER was measured the second week of July prior to anthesis on the most recently collared leaf. In 1981, CER measurements were made July 17-22, in most cases during anthesis, on the ear leaf. Crosbie et al. (1977) reported a genotypic correlation of 0.90 between CERs measured during the vegetative and grain-filling growth stages. Three plants per subplot were sampled. CER was calculated and expressed as mg CO_2 dm^{-2} $hour^{-1}$ employing the method of Hesketh and Moss (1963).

Plant architecture

Data were taken on several plant traits to characterize the plant architecture of the hybrids. Plant height, ear height, leaf area, and leaf orientation were determined on five competitive plants in each subplot. At plant maturity, plant and ear heights were measured as distances in cm from the soil surface to the collar of the flag leaf and to the point of primary ear attachment, respectively. The length and the maximum width of the eighth leaf below the tassel were determined during grain filling. Leaf area (A) was calculated as the product of leaf length and maximum leaf width multiplied by 0.75 (Montgomery, 1911). Leaf area (A) was multiplied by 9.39, a leaf area factor developed by Pearce et al. (1975), to provide an estimate of total leaf area per plant (dm^2).

The leaf orientation value (LOV) was suggested by Pepper

et al. (1977) to characterize leaf orientation:

$$LOV = \theta \frac{l_f}{l_t} \quad ,$$

where θ = leaf angle at the stalk from the horizon, l_f = leaf length to the point at which the leaf surface is parallel to the horizon, and l_t = total leaf length. Appropriate measurements were made on both the second leaf above the ear and the second leaf below the ear in order to characterize the leaf canopy both above (LOVA) and below the ear (LOVB).

Leaf area index (LAI) was calculated for each subplot by multiplying mean total leaf area per plant by the number of plants per subplot and dividing by the total soil surface area (dm^2) per subplot.

During the grain-filling period, the number of tillers in the two center rows of each subplot was determined. This count was expressed as the percentage of plants with tillers.

Flowering traits

Dates on which 25, 50, and 75% of the plants in the left-center row of each subplot displayed incipient silk extrusion and pollen shed, i.e., dehiscent anthers at least halfway down the central tassel branch were recorded. These dates were expressed as days from July 1. The number of heat units accumulated from planting to 50% silk also was calculated. A pollen-shed-to-silking interval was calculated for

each subplot by subtracting the date of 50% silk extrusion from the date of 50% pollen shed. The numbers of days between 25 and 75% silk extrusion and pollen shed were used as an expression of the silk-extrusion and pollen-shed intervals.

Dry matter determinations

Immediately after seedling vigor ratings were taken, ten random plants in the left-border row of each subplot were cut off at the soil surface and dried to constant weight. Dry weights were expressed on per plant and per hectare bases. Total above-ground dry matter was determined at the end of the vegetative period, designated as the date of 50% silk, also. On the day following the date on which a subplot was determined to be at 50% silk, five plants in the right-border row of that subplot were cut near the soil surface and dried in a forced-air dryer to constant weight. Estimates of dry matter per plant and dry matter per hectare were determined.

Partitioning to the ear-sink

To determine the date of black layer formation, five kernels per ear were sampled from ten competitive plants in the left-border row of each subplot beginning approximately 45 days after silk extrusion. Kernels were sampled from the midsection of the ear, split lengthwise on the center of the germinal-abgerminal plane, and examined for the development of the black layer. The kernels were sampled every

other day from alternate rows of the ear. The date (days from September 1) when all kernels from five of the ten plants displayed a black layer, illustrated as Phase 5 by Rench and Shaw (1971), was recorded as the subplot date of black layer formation. Duration of the grain-filling period was calculated as both the number of days and the number of accumulated heat units between the date of 50% silk extrusion and the date of black layer formation. Number of heat units was calculated by the formula (Gilmore and Rogers, 1958):

$$\text{Heat units during grain filling} = \sum_{i=1}^{n} [(T_i^H + T_i^L)/2 - 10]$$

where:

i = 1, ..., n indicates each day for the grain-filling period

T_i^H = maximum daily temperature (C) or 30C if C > 30C

T_i^L = minimum daily temperature (C) or 10C if C < 10C.

Temperature data for Ames were obtained from Mr. Ray Nicholson, Superintendent of the Agronomy and Agricultural Engineering Research Center. Temperature data for Ankeny were obtained from Dr. Nicholas Frey, Research Plant Physiologist, Pioneer Hi-Bred International, Inc., Johnston, Iowa.

Following black layer formation, five competitive plants with ears in the right-center row of each subplot were cut near the soil surface. From these five plants, all ears were harvested and the remaining vegetative portion was chopped with a portable, mechanical chopper (Diadem Brush Chopper, Model 316,

Vandermolen Corp., Livingston, New Jersey). Both the ears and vegetative portion were dried to constant weight in a forced-air dryer. A combined weight was determined to give total dry matter weight per plant. Dry matter yield at harvest was determined by multiplying dry matter per plant by the number of plants in the right-center row, dividing by the land area represented by the row and converting to metric tons per hectare. Ears from each subplot were shelled and grain weight was determined. Grain weight per plant was divided by dry matter per plant to provide a percentage estimate of harvest index.

To compare the amount of photosynthetically active tissue in the maize hybrid plants at the end of the grain-filling period, a visual rating of the left-border row was made. Each subplot was given a rating between 1 and 9, where 1 indicated complete discoloration of stalk and leaf tissue and 9 indicated little to no discoloration of stem and leaf tissue.

Ear-sink traits

Prior to shelling, ears harvested from the above plants were counted and total length and diameter of all ears were measured. Dividing total ear length and diameter by total number of ears estimated average ear length and ear diameter. After shelling, total diameter of the cobs was measured to calculate an average cob diameter. Kernel depth was

determined by subtracting cob diameter from ear diameter and dividing by two. A 300-kernel sample was weighed for each subplot. Weight per kernel was calculated and divided into total grain weight per plant to estimate number of kernels per plant.

Harvest traits

Immediately prior to harvest, counts were made of plants in the left-center row of each subplot broken below the ear and inclined more than 30^{o} from the vertical. These counts, divided by the total number of plants in the left-center row, gave the percentages of stalk and root lodging, respectively.

At harvest, all ears from plants in the left-center row of each subplot were hand-harvested. Ears judged to be machine-harvestable were harvested separately from those which were not machine-harvestable. Dropped ears and ears attached to stalks lodged below the third node were considered not machine-harvestable. Ears with less than 25% of their surface covered with kernels were considered barren and were discarded. Total number of ears per plant was calculated by dividing total number of ears by the number of plants in the left-center row. The number of machine-harvestable ears divided by the number of plants in the left-center row gave the number of machine-harvestable ears per plant.

Machine-harvestable and not machine-harvestable ears for

each subplot were shelled separately by machine with grain moisture and grain weight being determined at that time. Total and machine-harvestable grain weights were divided by the number of plants in the left-center row to give total and machine-harvestable grain yield per plant. Total and machine-harvestable grain weights were also multiplied by the number of rows per hectare to estimate total and machine-harvestable grain yield (q/ha), respectively.

Heat unit efficiency traits

The efficiency with which plants utilized heat units to produce dry matter was calculated for each subplot. Dry matter production per heat unit (g/plant/heat unit) during an early growth stage (VEG1) was obtained by dividing dry matter per plant at a seedling stage by number of heat units accumulated between the planting date and the date on which the seedling dry matter was determined. Dry matter production per heat unit(g/plant/heat unit) during the period between the seedling stage and 50% silk (VEG2) was determined by dividing the difference between dry matter per plant at 50% silk and the seedling stage by number of heat units accumulated between the date on which seedling dry matter was determined and the date of 50% silk. Dry matter production per heat unit (g/plant/heat unit) during the vegetative period (VEG3) was determined by dividing dry matter per plant at 50% silk by number of heat units accumulated between the

planting date and date of 50% silk. Total dry matter production per heat unit (g/plant/heat unit) during grain filling (GF) was calculated by dividing the difference between dry matter per plant at harvest and at 50% silk by number of heat units accumulated during grain filling. Vegetative dry matter production per heat unit (g/plant/heat unit) during grain filling (VEGGF) was determined by dividing vegetative dry matter production during grain filling by number of accumulated heat units during grain filling. Rate of grain filling per heat unit (g/plant/heat unit) was obtained by dividing total grain per plant by number of heat units accumulated during grain filling.

Statistical Analyses

Data were combined across all environments, i.e., a particular location in a particular year. Analyses of variance were computed for all traits without partitioning years and locations. A Mixed Model (Ostle, 1963) was assumed with environments being random while plant density levels and maize hybrids were fixed. The model used for these analyses was:

$$Y_{ijkl} = m + E_i + (R/E)_{ij} + D_k + (ED)_{ik} + \alpha_{ijk} + H_l + (EH)_{il} + (DH)_{kl} + (EDH)_{ikl} + \beta_{ijkl}$$

where:

Y_{ijkl} = observed value of the $ijkl^{th}$ subplot

m = experiment mean

E_i = effect of the i^{th} environment; $i = 1,2,3,4$

$(R/E)_{ij}$ = effect of the j^{th} replication within the i^{th} environment; $j = 1,2,3$

D_k = effect of the k^{th} plant density level; $k = 1,2,3$

$(ED)_{ik}$ = effect of the interaction of the i^{th} environment with the k^{th} plant density level

α_{ijk} = main plot error (error a)

H_l = effect of the l^{th} hybrid; $l = 1,\ldots,24$

$(EH)_{il}$ = effect of the interaction of the i^{th} environment with the l^{th} hybrid

$(DH)_{kl}$ = effect of the interaction of the k^{th} plant density level with the l^{th} hybrid

$(EDH)_{ikl}$ = effect of the interaction of the i^{th} environment and the k^{th} plant density level with the l^{th} hybrid

β_{ijkl} = residual error (error b).

Components of the combined analyses of variance are indicated in Table 4. Where main and interaction effects were significant, differences between means were detected with appropriate LSD values. Because our primary interest was in differences between decades of hybrids, the sums of

Table 4. Components of the combined analyses of variance for hybrid-plant density analysis

Source	df	E(MS)[a]
Environments (E)	e-1	
Replications/E	e(r-1)	
Densities (D)	d-1	$\sigma_b^2 + he\sigma^2_{(R/E)D} + rh\sigma^2_{DE} + reh\frac{\Sigma D^2}{d-1}$
D x E	(d-1)(e-1)	$\sigma_b^2 + he\sigma^2_{(R/E)D} + rh\sigma^2_{DE}$
Error a	e(r-1)(d-1)	$\sigma_b^2 + he\sigma^2_{(R/E)D}$
Hybrids (H)	h-1	$\sigma_b^2 + rd\sigma^2_{HE} + red\frac{\Sigma H^2}{h-1}$
H x E	(h-1)(e-1)	$\sigma_b^2 + rd\sigma^2_{HE}$
H x D	(h-1)(d-1)	$\sigma_b^2 + r\sigma^2_{HDE} + re\frac{\Sigma(HD)^2}{(h-1)(d-1)}$
H x D x E	(h-1)(d-1)(e-1)	$\sigma_b^2 + r\sigma^2_{HDE}$
Error b	ed(r-1)(h-1)	σ_b^2
Total	erdh-1	

[a]Environments were random, and densities and hybrids were fixed effects.

squares for hybrids, the hybrid x environment interaction, and the hybrid x density interaction were partitioned as indicated in Table 5. Orthogonal polynomials were used to calculate linear, quadratic, cubic, and quartic regression coefficients, i.e., b_l, b_q, b_c, and b_{LF} (Cochran and Cox, 1957). These regression coefficients allowed characterization of the response of various traits in maize hybrids to 40 years of breeding. The change across decades of traits for which the quartic regression model best described variation in decade means was considered uninterpretable. The quartic regression model, therefore, was designated as lack of fit. Linear and quadratic regression coefficients, i.e., b_{lin} and b_{quad}, also were calculated to characterize the response of various traits in maize hybrids to increased plant density.

Standard errors for b-values were calculated by the formula:

$$S_b = \left(\frac{S^2}{\sum_{i=1}^{n} X_c^2}\right)^{-\frac{1}{2}}$$

where:

S_b = standard error

S^2 = S^2_{HxE} (from analyses of variance) for regression coefficients across decades of hybrids and error b (from analyses of variance) for regression coefficients across plant densities.

Table 5. Partitioning of sums of squares for hybrids, hybrid x environment interaction and hybrid x density interaction

Source	Degrees of freedom		
Hybrids (H)	23		
Among decades (T)		5	
Among public decades (T_P)			4
Public decades linear (T_PL)			1
Public decades quadratic (T_PQ)			1
Public decades cubic (T_PC)			1
Public decades lack of fit (T_PLF)			1
Public 1970 vs proprietary 1970 (1970 vs Prop 1970)			1
Within decades of hybrids (H/T)		18	
H/1930			3
H/1940			3
H/1950			3
H/1960			3
H/1970			3
H/Prop 1970			3
Hybrid x environment (H x E)	69		
T x E		15	
T_P x E			12
T_PL x E			3
T_PQ x E			3
T_PC x E			3
T_PLF x E			3
1970 vs Prop 1970 x E			3
H/T x E		54	
H/1930 x E			9
H/1940 x E			9
H/1950 x E			9
H/1960 x E			9
H/1970 x E			9
H/Prop 1970 x E			9

Table 5. (Continued)

Source	Degrees of freedom
Hybrid x density (H x D)	46
T x D	10
T_P x D	8
T_PL x D	2
T_PQ x D	2
T_PC x D	2
T_PLF x D	2
1970 vs Prop 1970 x D	2
H/T x D	36
H/1930 x D	6
H/1940 x D	6
H/1950 x D	6
H/1960 x D	6
H/1970 x D	6
H/Prop 1970 x D	6

X_c = orthogonal polynomial coefficients

c = degree of polynomial; c = 1 for linear, 2 for quadratic and 3 for cubic

i = 1 ... n where n = the number of subplots on which the trait was measured for each decade of hybrids.

Standard errors for testing differences between regression coefficients (S_a) were computed by multiplying S_b by $\sqrt{2}$.

RESULTS

Harvest Traits

The data for harvest traits are presented in Tables 6-16 and illustrated by Figures 1-8. The influence of environment on harvest traits is illustrated by means in Table 6. The best environment for both total grain yield and machine-harvestable grain yield occurred at Ames in 1980 with means of 88.3 and 81.8 q/ha, respectively. These high production conditions, however, were not repeated at Ames in 1981, where total and machine-harvestable grain yields were lowest at 64.2 and 57.7 q/ha, respectively. Root lodging varied from only 1.2% at Ankeny in 1981 to 18.4% at Ames in 1980. Likewise, stalk lodging ranged from 6.8% at Ankeny in 1980 to 20.2% at Ankeny in 1981. Grain moisture was significantly higher at Ames in 1981 (Table 6) than at the other environments which were not significantly different from one another.

Plant density effects on total or machine-harvestable grain yield were not significant because density x environment interactions were large (Table 8). Total grain yield per plant at low plant density was 110.9 g higher than at high plant density (Table 6). A significant difference of 114.1 g for machine-harvestable grain also was observed between low and high plant density (Table 6). As expected, both stalk and root lodging increased as plant density increased (Table 6).

Table 6. Means for harvest traits of 24 single-cross hybrids grown at three plant densities in four environments

	Total grain yield (q/ha)	MH[a] grain yield (q/ha)	Total grain per plant (g)	MH grain per plant (g)	Root lodging (%)	Stalk lodging (%)	Grain moisture (%)
Ames 1980	88.3	81.8	216.9	202.5	18.4	7.9	14.8
Ames 1981	64.2	57.7	166.1	150.5	4.5	15.7	21.6
Ankeny 1980	71.3	68.3	164.0	157.9	7.3	6.8	16.9
Ankeny 1981	77.7	68.2	193.6	172.4	1.2	20.2	17.8
$LSD_{0.05}$	13.1	11.9	27.1	24.6	5.5	3.1	3.8
Density L[b]	71.4	67.6	246.7	233.9	4.7	9.2	15.3
Density M	77.9	70.7	178.7	162.1	7.8	14.1	17.3
Density H	77.5	68.5	135.8	119.8	11.2	16.2	17.9
$LSD_{0.05}$	11.8	10.8	24.4	22.2	5.0	2.8	3.4
Overall $\bar{X}$	75.6	68.9	186.9	171.8	7.9	13.1	17.8
C.V. (%)	16.5	17.5	16.7	18.2	127.1	78.4	5.9

[a]MH = machine-harvestable in this and all tables where applicable.

[b]Hereinafter, L, M, and H denote low, medium, and high plant densities as specified in Table 3.

Table 7. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for harvest traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in four environments

Decades of hybrids	Total grain yield (q/ha)	MH grain yield (q/ha)	Total grain per plant (g)	MH grain per plant (g)	Root lodging (%)	Stalk lodging (%)	Grain moisture (%)
1930	64.5	47.0	159.8	118.7	16.9	33.6	17.5
1940	73.8	61.7	186.3	158.1	8.8	23.3	17.6
1950	74.9	70.8	185.3	177.1	7.5	8.5	17.1
1960	75.4	74.5	188.9	186.7	5.8	3.7	18.8
1970	87.9	84.5	214.7	207.5	6.3	6.0	18.7
Prop 1970	77.4	75.2	187.4	182.9	1.8	3.7	17.1
$LSD_{0.05}$	5.4	7.4	13.0	14.7	5.5	8.5	0.5
b_1[a]	4.8±0.6	8.8±0.7	11.2±1.5	20.6±1.7	-2.4±0.6	-7.5±0.6	0.4±0.05
b_q	0.4±0.5	-1.1±0.6	0.3±1.2	-3.3±1.4	1.2±0.5	2.5±0.5	0.1±0.04
b_c	2.0±0.6	1.2±0.7	4.8±1.5	3.2±1.7	-0.5±0.6	1.2±0.6	-0.1±0.05

[a]Hereinafter, b_1, b_q, and b_c are regression coefficients representing response across decades of hybrids.

Table 8. Mean squares from combined analyses of variance for harvest traits of maize hybrids grown at three plant densities in four environments

Source	df	Mean squares	
		Total grain yield	MH grain yield
Environment (E)	3	21705.6	20638.2
Reps/E	7[a]	1637.2	952.2
Density (D)	2	3518.0	639.5
D x E	6	3092.9**	2546.5**
Error a	14	291.1	279.8
Hybrid (H)	23	3286.0**	6621.0**
H x E	69	484.7*	582.2**
H x D	46	434.3**	557.8**
H x D x E	138	170.4	166.4
Error b[b]	482	156.6	146.1

[a]Only two replications were used in the 1980 Ankeny environment due to herbicide damage in some subplots of the third replication.

[b]Degrees of freedom for error b: total grain yield, 471; MH grain yield, 471; total grain per plant, 471; MH grain per plant, 471; percentage root lodging, 482; percent stalk lodging, 482; grain moisture, 478.

*,**Significant at the 5% and 1% levels of probability, respectively, in this and all following tables.

Mean squares				
Total grain per plant	MH grain per plant	Root lodging	Stalk lodging	Grain moisture
121063.0	106953.7	11964.4	7939.0	2973.2
8960.6	5688.5	338.4	359.0	117.0
816432.5**	869512.8**	2753.4	3443.9**	88.7
13260.4**	10996.6**	1133.0	266.4	255.6**
1453.1	1212.5	602.2	218.3	48.5
18525.8**	39064.0**	2538.6**	6442.4**	443.6**
2830.6**	3597.7**	502.0**	411.0**	56.1**
1713.4**	2913.5**	140.6*	280.9**	57.1*
958.1	1098.8	113.0	155.5**	36.1
979.7	974.4	100.5	106.2	36.9

Table 9. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for harvest traits (Table 8)

Source	df	Mean squares: Total grain yield	Mean squares: MH grain yield
Hybrid	23	3286.0**	6621.0**
Decades	5	8773.3**	22230.4**
Public decades	4	9153.9**	26377.2**
Linear	1	30911.4**	101344.7**
Quadratic	1	298.7	2059.9
Cubic	1	5367.5**	1843.7
Lack of fit	1	38.0	260.7
1970 vs Prop 1970	1	7251.1**	5643.0*
Hybrids/decades	18	1761.8**	2285.0**
H/1930	3	4120.5**	7120.5*
H/1940	3	435.2	902.1
H/1950	3	394.2	231.8
H/1960	3	447.9	467.0
H/1970	3	3594.8**	3469.5**
H/Prop 1970	3	1578.2*	2185.8**

Mean squares				
Total grain per plant	MH grain per plant	Root lodging	Stalk lodging	Grain moisture
18525.8**	39064.0**	2538.6**	6442.4**	60.2**
48683.1**	126939.3**	2446.9**	17695.3**	95.1**
48795.5**	148731.1**	2730.4**	22026.9**	78.2**
164327.5**	560994.7**	7807.1**	73977.1**	166.4**
212.5	20558.7*	2652.9*	11792.2**	33.0**
30489.0**	13218.8	273.2	1787.6	19.8*
153.1	152.5	188.4	550.8	93.8**
48233.5**	39771.9**	1312.7	368.6	162.7**
10148.8**	14654.2**	2564.1**	3316.6**	50.5**
29069.6**	53028.9**	10305.9*	14239.9**	77.0**
1010.4**	2715.5	212.7	3727.7**	8.7
3754.3	2293.4	3013.7**	871.3**	1.7
1091.4	1114.1	810.6	135.5	8.8
16566.9**	16148.3**	876.5	405.9	131.3**
9400.2*	12624.9*	165.2	519.2	75.2**

Table 10. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for harvest traits of maize hybrids (Table 8) grown at three plant densities in four environments

Source	df	Mean squares: Total grain yield	Mean squares: MH grain yield
Hybrid x environment (E)	69	484.7*	582.2**
Decades x E	15	597.7*	906.9**
Public decades x E	12	687.6**	1054.0**
Linear x E	3	469.1*	1354.3**
Quadratic x E	3	422.3*	493.2*
Cubic x E	3	1526.5**	2058.7**
Lack of fit x E	3	332.7	309.9
1970 vs Prop 1970 x E	3	237.8	318.3
Hybrids ($\bar{H}$)/decades x E	54	453.3**	492.1**
H/1930 x E	9	334.2*	1546.3**
H/1940 x E	9	305.5*	510.1**
H/1950 x E	9	107.7	191.4
H/1960 x E	9	956.9**	924.6**
H/1970 x E	9	678.8**	536.4**
H/Prop 1970 x E	9	336.5*	297.6*

Mean squares				
Total grain per plant	MH grain per plant	Root lodging	Stalk lodging	Grain moisture
2830.6**	3597.7**	502.0**	411.0**	3.8**
3010.2**	5084.8**	356.0**	1211.2**	4.0**
3614.7**	6128.4**	323.5**	1503.1**	4.7**
3160.0*	9378.5**	519.5**	3762.2**	4.0**
3088.4*	3046.0*	147.5	367.2*	1.7
6392.7**	9972.3**	357.0*	1434.6**	11.2**
1817.6	2116.8	270.2*	448.3**	2.0
592.2	910.5	485.6**	43.6	1.1
2780.7**	3184.6**	542.6**	188.7**	3.8**
2202.2*	4011.8**	1691.2**	274.1**	7.9**
1800.7	3364.5**	263.6**	438.9**	2.0
947.7	1173.6	472.1**	68.0	2.4*
6077.2**	5912.8**	437.5**	38.5	1.4
3417.8**	2467.8**	344.0**	162.6	3.2**
2238.7*	2176.7*	47.0	116.8	5.7**

Table 11. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for harvest traits of maize hybrids (Table 8) grown at three plant densities in four environments

Source	df	Mean squares: Total grain yield	Mean squares: MH grain yield
Hybrid x density (D)	46	434.3**	557.8**
Decades x D	10	1172.4**	1386.5**
Public decades x D	8	1258.6**	1616.1**
Linear x D	2	4054.9**	5797.1**
Quadratic x D	2	219.8	419.5
Cubic x D	2	657.9*	23.3
Lack of fit x D	2	101.9	224.6
1970 vs Prop 1970 x D	2	827.4**	468.1*
Hybrids (H)/decades x D	36	229.3	327.6**
H/1930 x D	6	45.3	327.8*
H/1940 x D	6	525.7**	739.2**
H/1950 x D	6	298.0	349.5*
H/1960 x D	6	60.8	62.2
H/1970 x D	6	247.2	277.2
H/Prop 1970 x D	6	198.6	209.7

Mean squares				
Total grain per plant	MH grain per plant	Root lodging	Stalk lodging	Grain moisture
1713.4**	2913.5**	140.6*	280.9**	1.9
1787.5	2171.2*	135.4	311.3*	2.1
2216.3*	2694.4**	106.3	383.4*	2.5
5789.1**	5612.4**	164.1	375.9	2.0
322.1	3034.9*	43.8	219.0	0.6
2163.5	489.0	184.8	909.7**	2.2
590.4	1641.4	32.4	29.1	5.1**
72.2	78.3	251.7	23.0	0.5
1692.8*	3119.7**	142.0	272.5*	1.8
2312.6*	9244.0**	346.8**	935.1**	2.2
3359.1**	4771.1**	97.5	325.1	1.3
1925.2	2138.8*	132.2	83.3	2.0
454.9	476.9	83.3	17.4	0.8
590.4	609.4	106.5	237.3	3.6**
1514.7	1477.8	85.8	36.8	1.0

Table 12. Environment x decade means for total grain yield of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
	q/ha				
1930	46.8	58.2	68.6	82.0	35.2
1940	68.0	67.9	71.6	87.0	19.0
1950	62.2	74.4	80.6	82.3	20.1
1960	60.7	72.2	81.3	87.0	26.3
1970	80.4	84.6	86.5	99.1	18.7
Prop 1970	67.1	70.0	77.3	93.0	25.9
$\bar{X}$	64.2	71.3	77.7	88.3	

$LSD_{0.05}$ = 5.8 q/ha across environments within a decade

Table 13. Environment x decade means for machine-harvestable grain yield of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
	q/ha				
1930	26.7	52.5	45.2	65.6	38.9
1940	55.3	63.3	53.3	76.6	23.3
1950	59.2	70.9	74.4	79.0	19.8
1960	60.2	71.8	79.7	85.9	25.7
1970	78.2	83.2	81.4	95.0	16.7
Prop 1970	66.5	67.7	75.1	89.2	22.7
$\bar{X}$	57.7	68.3	68.2	81.8	

$LSD_{0.05}$ = 5.6 q/ha across environments within a decade

Table 14. Environment x decade means for percentage root lodging of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ankeny 1981	Ames 1981	Ankeny 1980	Ames 1980	Range
			%		
1930	4.3	17.5	14.0	31.0	26.6
1940	1.3	1.5	9.1	23.4	22.1
1950	0.7	4.6	8.3	16.8	16.0
1960	0.1	1.9	1.7	18.0	17.9
1970	0.4	1.1	8.3	16.1	15.8
Prop 1970	0.2	0.2	2.2	4.8	4.6
$\bar{X}$	1.2	4.5	7.3	18.4	

$LSD_{0.05}$ = 4.6% across environments within a decade

Table 15. Environment x decade means for percentage stalk lodging of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ankeny 1980	Ames 1980	Ames 1981	Ankeny 1981	Range
			%		
1930	21.1	22.5	38.4	48.4	27.3
1940	6.3	12.0	28.3	40.9	34.5
1950	5.5	6.1	9.7	11.7	6.2
1960	2.0	2.9	6.6	2.5	4.6
1970	3.6	2.2	7.2	10.3	8.1
Prop 1970	2.2	1.6	3.2	7.2	5.6
$\bar{X}$	6.8	7.9	15.7	20.2	

$LSD_{0.05}$ = 4.8% across environments with a decade

Table 16. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for harvest traits for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrids	Density L	Density M	Density H	b_{lin} [a,b]	b_{quad}
	Total grain yield (q/ha)				
1930	68.3	63.4	62.0	-3.2	0.6
1940	71.4	77.4	72.8	0.7	-1.8
1950	70.1	78.3	76.2	3.1	-1.7
1960	71.9	77.3	77.1	2.6	-0.9
1970	75.4	91.6	96.7	12.0	-1.9
Prop 1970	71.3	80.3	80.4	4.6	-1.5
$LSD_{0.05}$	5.3	5.3	5.3	3.9	2.2
	MH grain yield (q/ha)				
1930	54.2	44.3	43.1	-11.1	1.45
1940	66.3	61.7	57.0	-4.7	-0.02
1950	69.2	74.9	68.4	-0.4	-2.03
1960	71.8	76.9	74.8	1.5	-1.20
1970	74.4	88.6	90.6	8.1	-2.03
Prop 1970	70.1	78.2	77.1	3.5	-1.53
$LSD_{0.05}$	5.1	5.1	5.1	3.8	2.14
	Stalk lodging (%)				
1930	29.8	36.8	34.4	2.3	-1.57
1940	14.1	26.1	29.6	7.8	-1.45
1950	3.9	8.5	12.3	4.7	0.02
1960	2.7	3.5	4.8	1.1	0.08
1970	2.9	6.3	8.9	3.0	0.13
Prop 1970	1.7	3.3	6.0	2.2	0.18
$LSD_{0.05}$	5.2	5.2	5.2	3.7	2.14

[a]Hereinafter, b_{lin} and b_{quad} are regression coefficients representing the response across plant densities.

[b]Hereinafter, b_{lin} and b_{quad} are significantly different from zero if they are greater than their LSD divided by $\sqrt{2}$.

Table 16. (Continued)

Decade of hybrids	Density L	Density M	Density H	b_{lin}	b_{quad}
	Total grain yield per plant (grams)				
1930	231.0	144.2	108.1	-61.5	8.5
1940	248.4	178.4	129.0	-59.7	3.4
1950	244.3	179.4	133.8	-55.3	3.2
1960	251.4	177.2	136.9	-57.3	5.7
1970	264.5	211.1	167.1	-48.7	1.6
Prop 1970	239.4	183.6	140.0	-47.7	2.0
$LSD_{0.05}$	13.1	13.1	13.1	9.3	5.3
	MH grain yield per plant (grams)				
1930	182.1	100.4	75.0	-64.7	9.4
1940	230.7	141.9	100.8	-65.0	8.0
1950	241.0	171.6	119.9	-60.6	3.0
1960	251.0	176.3	132.8	-59.1	5.2
1970	261.0	204.1	156.4	-47.7	1.5
Prop 1970	235.7	179.5	134.2	-50.8	1.8
$LSD_{0.05}$	13.1	13.1	13.1	9.8	5.3

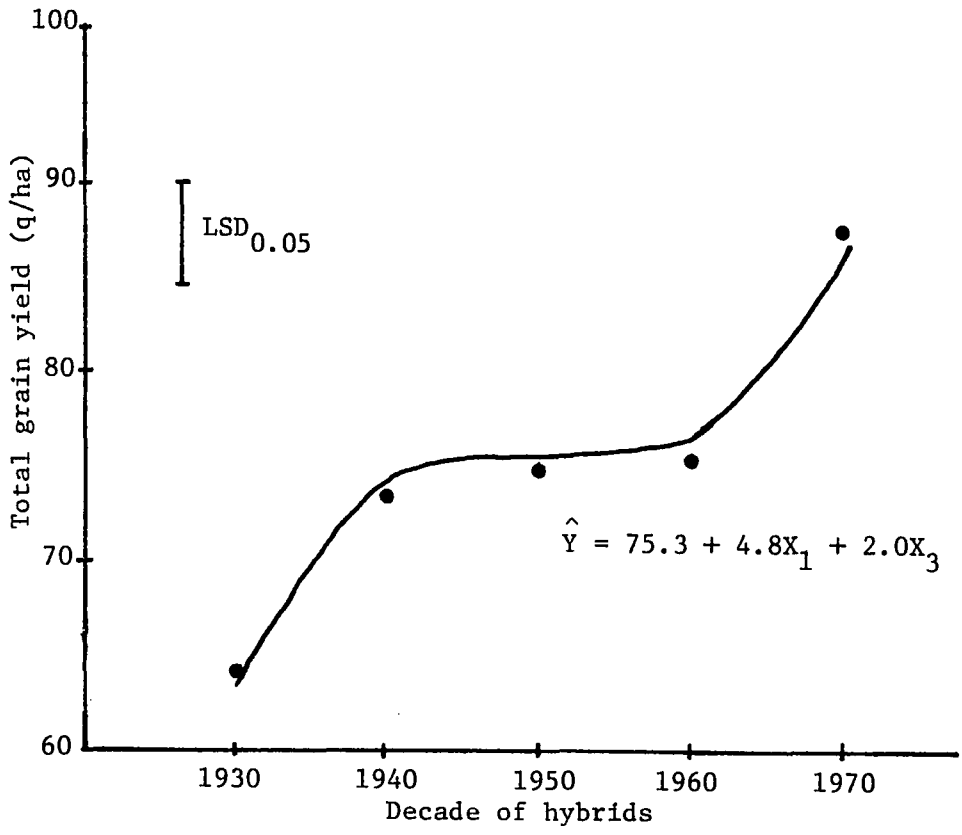

Figure 1. Predicted total grain yields for hybrids at 10-year intervals based on actual total grain yields of four public hybrids selected to represent each decade from 1930 to 1970

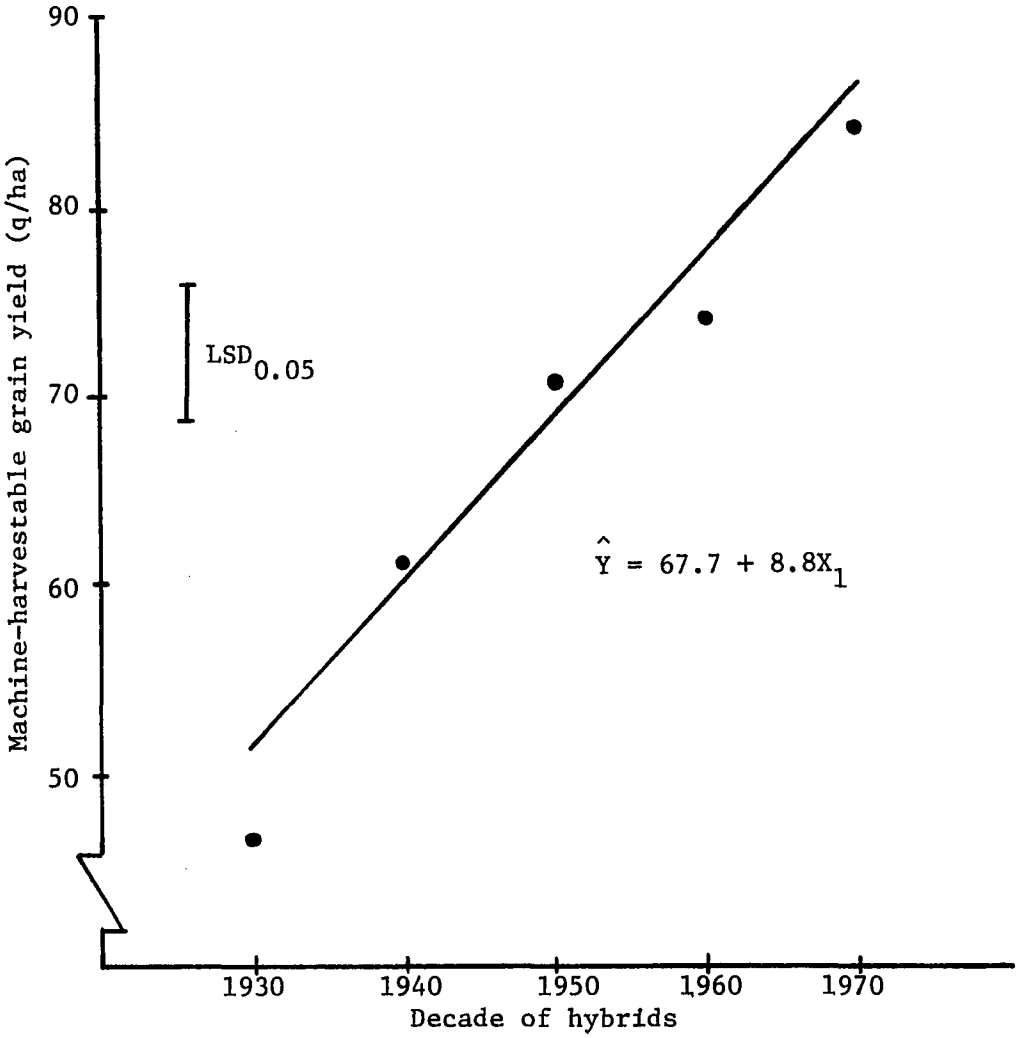

Figure 2. Predicted machine-harvestable grain yields for hybrids at 10-year intervals based on actual machine-harvestable grain yields of four public hybrids selected to represent each decade from 1930 to 1970

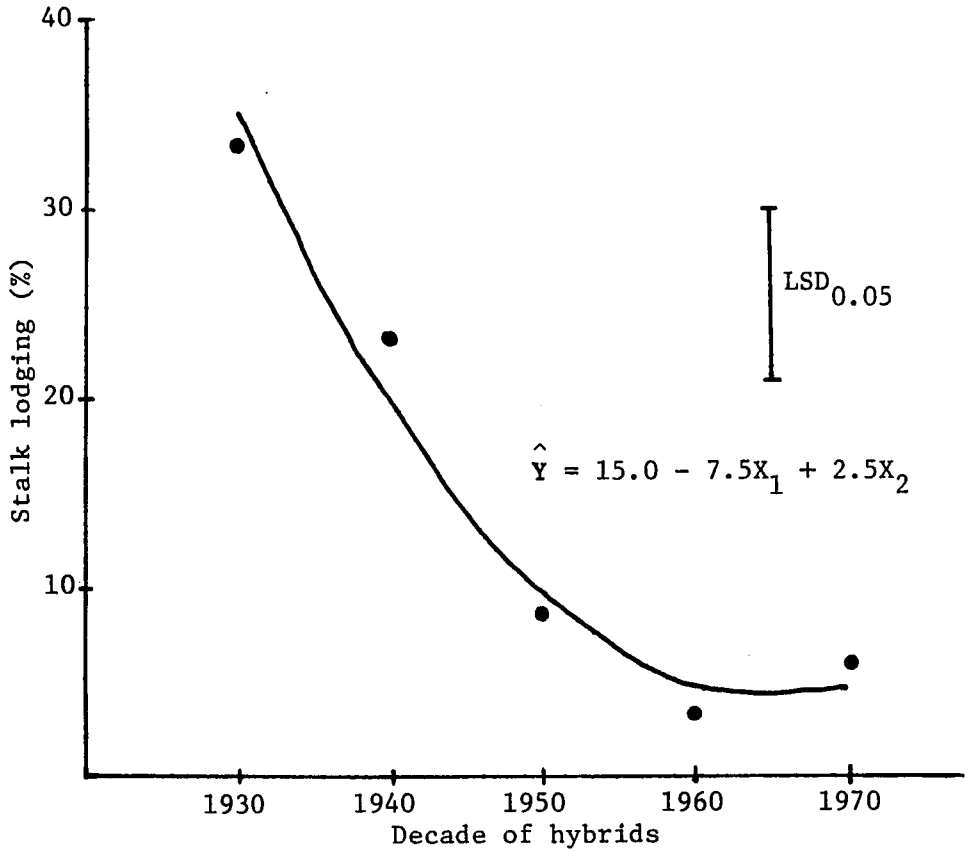

Figure 3. Predicted percentages of stalk lodged plants for hybrids at 10-year intervals based on actual percentages of stalk lodged plants of four public hybrids selected to represent each decade from 1930 to 1970

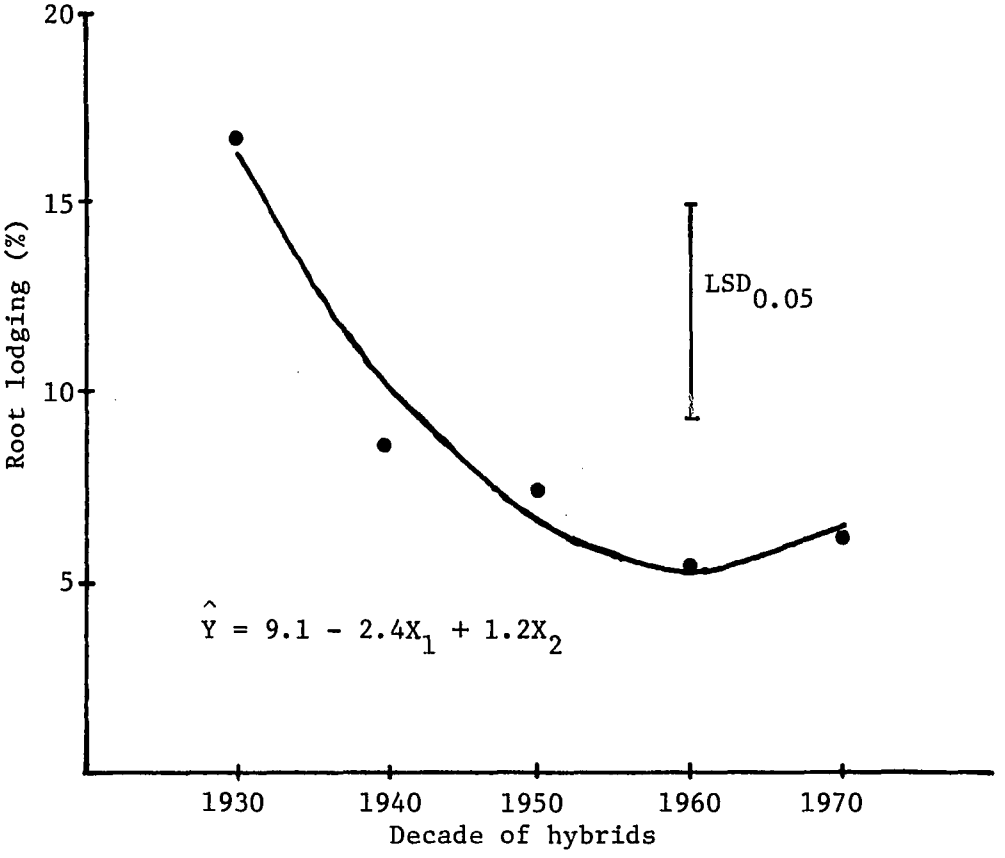

Figure 4. Predicted percentages of root lodged plants for hybrids at 10-year intervals based on actual percentages of root lodged plants of four public hybrids selected to represent each decade from 1930 to 1970

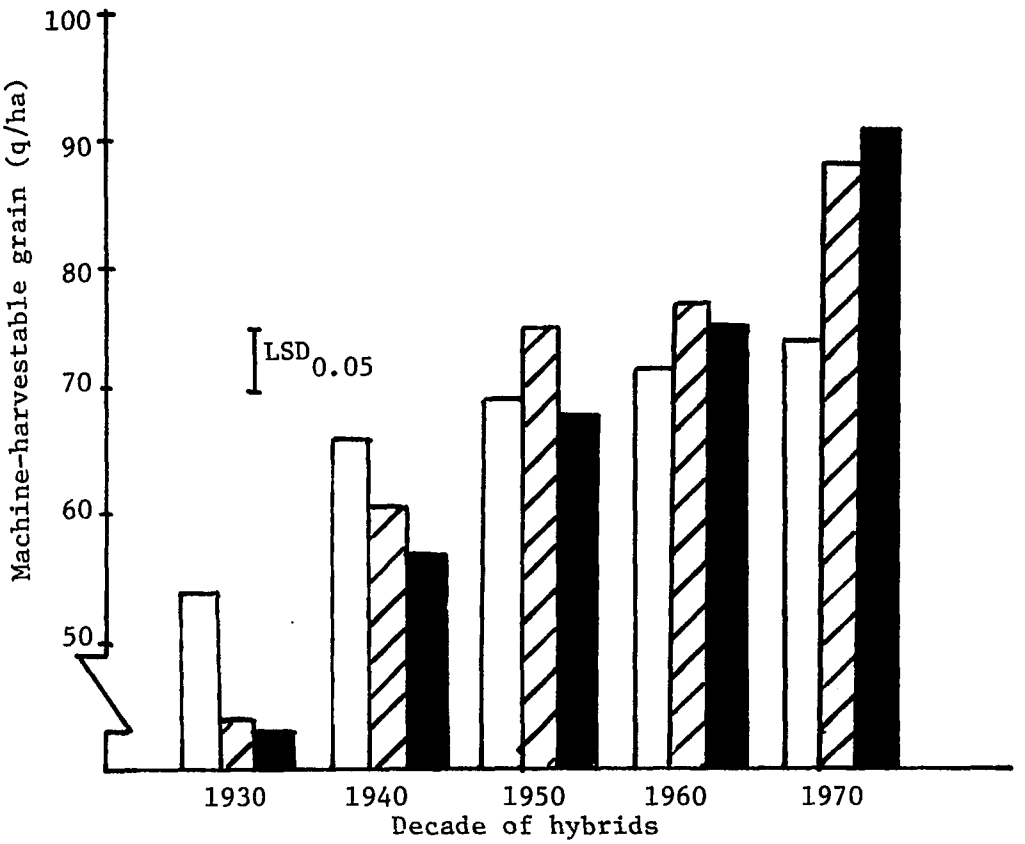

Figure 5. Mean machine-harvestable grain yields at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

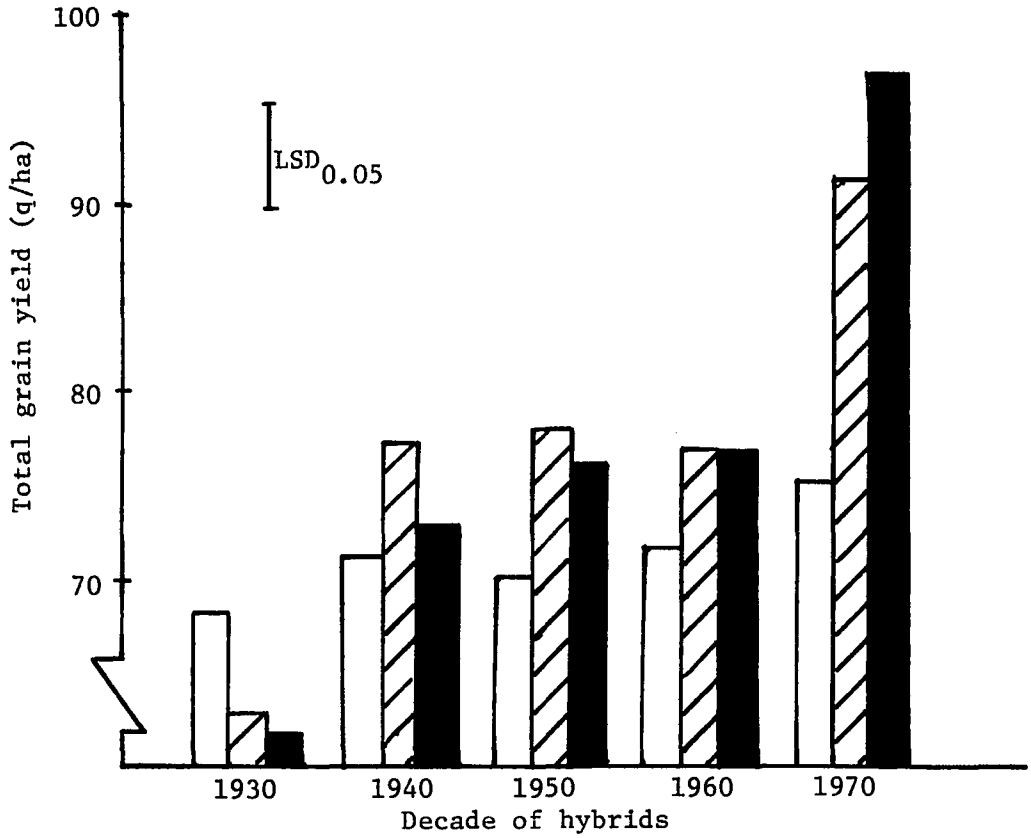

Figure 6. Mean total grain yields at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

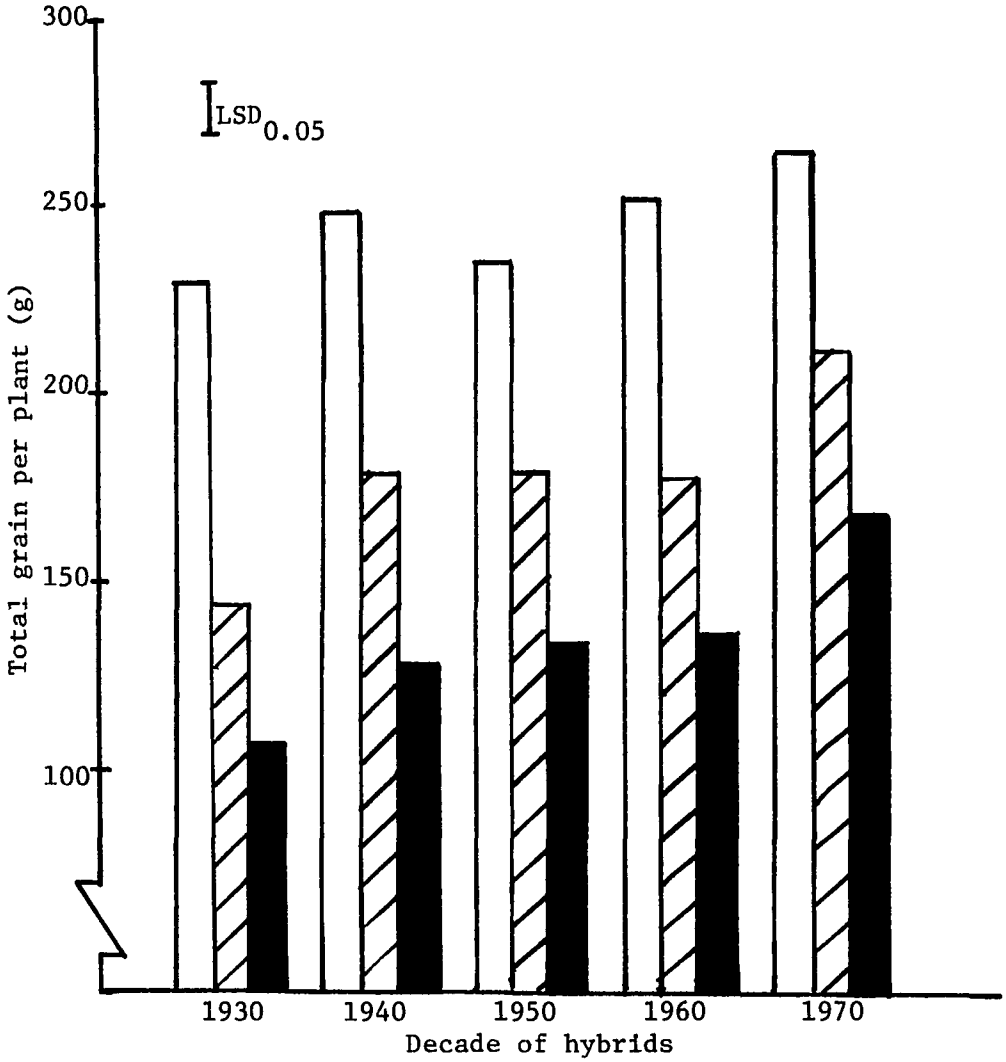

Figure 7. Mean total grain per plant at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

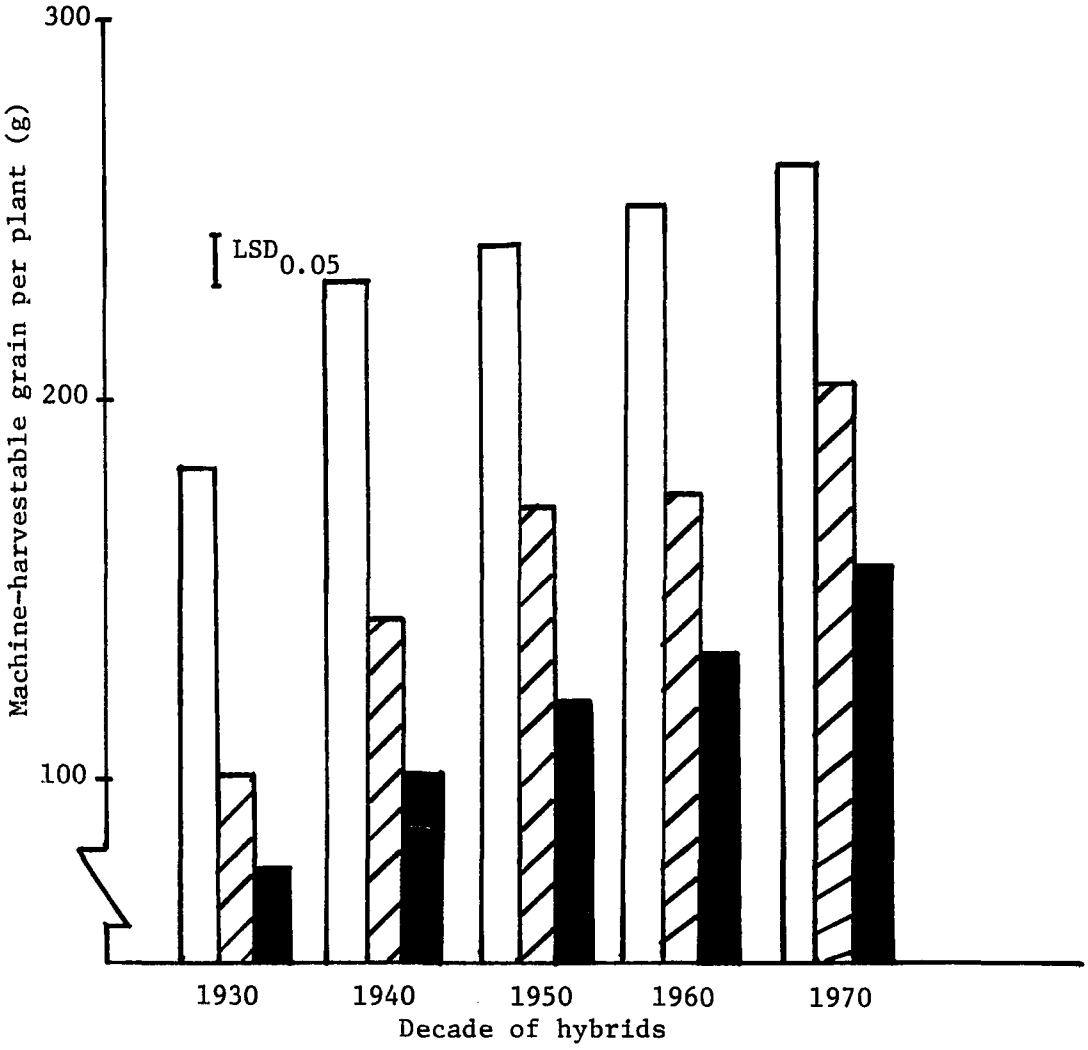

Figure 8. Mean machine-harvestable grain per plant at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

Mean squares from combined analyses of variance (Table 9) demonstrated that significant change in total grain yield across decades was primarily linear, but they also indicated a significant cubic response. Figure 1 illustrates this linear increase in total grain yield of 4.8 ± 0.6 q/ha/decade (Table 7). The cubic response also apparent in Figure 1 is due to a plateau between the 1940 and 1960 groups which was preceded and followed by significant increases in total grain yield.

The linear model also best described the significant change in machine-harvestable grain yield across groups of hybrids (Table 9, Figure 2). Machine-harvestable grain yields have increased, however, at approximately twice the rate of total grain production during the past 40 years, i.e., b_1 = 8.8 ± 0.7 q/ha/decade. These data suggest that 40 years of maize breeding have increased total grain yield 23.4 q/ha and machine-harvestable grain yield 37.5 q/ha (Table 7). Public hybrids representing the 1970 decade produced significantly greater total and machine-harvestable grain yields, i.e., 10.5 and 9.3 q/ha, respectively, than did their 1970 proprietary hybrid counterparts (Tables 7 and 9).

The 1970 decade of hybrids produced 54.9 g more total grain per plant and 88.8 g more machine-harvestable grain per plant than did the 1930 decade of hybrids (Table 7). If 54.9 g of the 88.8 g increase in machine-harvestable grain yield per plant was due to more total grain per plant, the

difference, i.e., 33.9 g, must be due to less lodging and better ear retention. Indeed, stalk and root lodging have decreased a significant 27.6 and 10.6%, respectively, over decades (Tables 7 and 9). The majority of variance among decade means for stalk and root lodging was best explained by a linear model (Table 9), but mean squares for the quadratic model were also significant. Linear regression coefficients of -7.5 ± 0.6% stalk lodging and -2.4 ± 0.6% root lodging per decade indicated a more successful decrease in stalk lodging (Table 7, Figures 3 and 4). But the levels of both stalk and root lodging in the 1970 hybrids are quite similar at 6.0 and 6.3%, respectively. Note that neither stalk nor root lodging decreased significantly after the 1950 decade (Table 7). The range of percentage of grain moisture among groups of hybrids was 1.7% (Table 7). Although grain moisture of the 1960 and 1970 hybrids was significantly higher statistically than the 1930, 1940, and 1950 hybrids (Table 9), the differences were not important practically. Similarity of percentage of grain moisture at harvest across the decades of hybrids suggested that their maturities were alike.

An indication of variation in harvest traits among hybrids within a decade is provided by mean squares in Table 9. Significant differences in all grain yield traits were observed only among hybrids of the 1930 and 1970 decades.

The public decades x environment interaction mean squares

were significant for all harvest traits (Table 10). Ames 1981 was the lowest total grain yield environment and Ames 1980 was the highest total grain yield environment for every decade (Table 12). The range across environments was 18.7 q/ha for the 1970 decade, which was approximately half that of the 1930 decade, i.e., 35.2 q/ha. A similar situation existed for machine-harvestable grain yields (Table 13). Table 15 indicates that hybrids of the 1950, 1960, and 1970 decades resisted stalk lodging better than did the 1930 and 1940 decade hybrids. The 1950, 1960, and 1970 decades of maize hybrids also displayed less root lodging at Ames 1980, i.e., the environment in which root lodging was most severe, than did their earlier counterparts (Table 14).

The relative responses by the public decades for all harvest traits except root lodging and grain moisture to different plant densities differed significantly (Table 11). Means in Table 16 showed that linear regression coefficients for total and machine-harvestable grain yield were negative for the early decades, but they were positive in later decades. As illustrated in Figure 5, the low plant density was the optimum environment for machine-harvestable yield for the first two decades, the medium plant density was optimum for 1950 and 1960 decades, and the 1970 decade produced greatest machine-harvestable grain yield at high plant density. Similar results were found for total grain yield (Figure 6). Note

that total grain yield improvement across decades was 34.7 q/ha at the high plant density compared to 7.1 q/ha at the low plant density (Table 16).

Linear regression coefficients for total and machine-harvestable grain yield per plant across plant densities were negative for all decades (Table 16). They increased significantly, however, from b = -61.5 g total grain/plant for the 1930 decade to b = -48.7 g total grain/plant for the 1970 decade (Table 16). This favorable change was due primarily to total grain yield improvements across decades at high plant densities. For example, the difference in total grain per plant between 1930 and 1970 decades was 33.5 and 59.0 g per plant at low and high plant densities, respectively. Although Figure 7 indicated significant increases in total grain per plant at the high plant density only between the 1930 and 1940 decades and the 1960 and 1970 decades, Figure 8 indicated a linear increase across decades of machine-harvestable grain per plant at the high plant density.

Plant Traits

Means and analyses of variance for plant traits are given in Tables 17-22. Ranges of 42.4 and 11.2 cm among environment means for plant and ear height, respectively, illustrate the effect of environment on these traits (Table 17). Plant density effects on plant height were not significant, but ear

Table 17. Means for plant traits of 24 single-cross hybrids grown[a] at three plant densities in four environments[a]

	Plant height (cm)	Ear height (cm)	Emergence (%)
Ames 1980	212.0	112.9	92.2
Ames 1981	199.7	116.6	92.9
Ankeny 1980	201.2	106.2	
Ankeny 1981	242.1	117.4	87.6
$LSD_{0.05}$	4.2	4.1	1.6
Density L	213.5	110.4	90.8
Density M	212.0	113.5	91.2
Density H	215.7	116.0	90.8
$LSD_{0.05}$	3.6	3.6	1.6
Overall $\bar{X}$	213.7	113.3	90.9
C.V. %	6.2	5.8	7.5

[a]Emergence determined in three environments.

Table 18. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for plant traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in four environments[a]

Decade of hybrids	Plant height (cm)	Ear height (cm)	Emergence (%)
1930	203.0	117.4	88.4
1940	206.8	111.5	91.1
1950	211.1	113.9	90.9
1960	223.8	113.4	90.0
1970	221.5	117.4	93.6
Prop 1970	211.2	106.1	91.5
$LSD_{0.05}$	3.7	2.7	2.6
b_1	4.4±0.4	0.2±0.3	0.9±0.3
b_q	0.4±0.1	1.2±0.1	0.1±0.2
b_c	-2.1±0.4	-0.4±0.3	0.7±0.3

[a]Emergence determined in three environments.

Table 19. Mean squares from combined analyses of variance for plant traits of maize hybrids grown at three plant densities in four environments[a]

Source	df	Mean squares		
		Plant height	Ear height	Emergence[b]
Environment (E)	2	83638.8	5598.4	1774.2
Reps/E	8	946.0	380.3	191.4
Density (D)	2	992.9	2333.0**	11.0
D x E	6	728.2	311.9**	41.2
Error a	16	337.0	33.1	67.7
Hybrid (H)	23	4148.5**	2903.3**	309.0**
H x E	69	255.2*	134.2**	88.0**
H x D	46	172.5	52.0	45.7
H x D x E	138	176.2	34.3	69.4**
Error b[c]	552	177.0	43.0	46.8

[a]Emergence determined in three environments.

[b]Refer to Appendix Table A1 for degrees of freedom for emergence.

[c]Degrees of freedom for error b: plant height, 552; ear height, 552; percent emergence, 414.

Table 20. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for plant traits (Table 19)

Source	df	Mean squares		
		Plant height	Ear height	Emergence
Hybrid	23	4148.5**	2903.3**	309.0**
Decades	5	8658.1**	2642.2**	356.5**
Public decades	4	8926.8**	994.4**	386.8**
Linear	1	27779.0**	53.6	946.1**
Quadratic	1	378.4	2980.8**	8.6
Cubic	1	6145.9**	230.4	579.7*
Lack of fit	1	1404.0*	712.8*	12.7
1970 vs Prop 1970	1	7583.0**	9233.3**	235.4
Hybrids/decades	18	2895.8**	2975.8**	295.8**
H/1930	3	1266.5**	3456.0**	268.7*
H/1940	3	3543.4**	3071.9**	712.8**
H/1950	3	2402.8**	3398.5**	80.4
H/1960	3	6696.2**	5447.6**	285.9*
H/1970	3	552.0	1109.3**	178.3
H/Prop 1970	3	2713.9**	1371.5**	248.5*

Table 21. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for plant traits of maize hybrids (Table 19) grown at three plant densities in four environments[a]

Source	df	Mean squares		
		Plant height	Ear height	Emergence[b]
Hybrid x environment (E)	69	255.2*	134.2**	88.0**
Decades x E	15	358.2*	192.5**	116.9**
Public decades x E	12	407.0**	138.2**	109.4*
Linear x E	3	400.3	166.6*	136.7
Quadratic x E	3	312.2	265.8**	38.5
Cubic x E	3	795.1**	35.5	0.3
Lack of fit x E	3	120.6	85.1	252.0**
1970 vs Prop 1970 x E	3	163.0	409.7**	147.0*
Hybrids/decades x E	54	226.6	118.0**	79.9**
H/1930 x E	9	468.1**	195.5**	123.6*
H/1940 x E	9	146.9	129.5**	38.5
H/1950 x E	9	124.0	64.3	33.7
H/1960 x E	9	408.5*	218.8**	169.9**
H/1970 x E	9	85.1	45.8	35.9
H/Prop 1970 x E	9	127.1	54.2	78.1

[a]Emergence was determined in three environments.

[b]Refer to Appendix Table A1 for degrees of freedom for emergence.

Table 22. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for plant traits of maize hybrids (Table 19) grown at three plant densities in four environments[a]

Source	df	Mean squares		
		Plant height	Ear height	Emergence
Hybrid x density (D)	46	172.5	52.0	45.7
Decades x D	10	96.2	51.2	34.1
Public decades x D	8	100.5	48.3	41.3
Linear x D	2	84.8	80.6	15.8
Quadratic x D	2	138.2	70.9	53.6
Cubic x D	2	49.4	13.8	43.5
Lack of fit x D	2	129.7	28.0	52.4
1970 vs Prop 1970 x D	2	78.7	62.6	5.3
Hybrids/decades x D	36	193.8	52.2	48.9
H/1930 x D	6	259.3	30.8	38.3
H/1940 x D	6	224.4	43.3	62.8
H/1950 x D	6	156.8	63.2	21.5
H/1960 x D	6	384.5*	85.1	90.4
H/1970 x D	6	56.5	48.9	49.0
H/Prop 1970 x D	6	81.0	41.7	31.6

[a]Emergence was determined in three environments.

height was 6.5 cm higher at the high plant density than at the low plant density.

The hybrids in the 1970 group were significantly taller, i.e., 18.5 cm, than their 1930 counterparts, but no difference in ear placement was observed (Table 18). The increase of plant height over decades was best described linearly with a regression coefficient of 4.4 ± 0.4 cm per decade (Table 20). Sums of squares for the quadratic regression model accounted for the largest proportion of the significant variation in public decade means for ear height (Table 20). Ear height was slightly reduced during the 1940 to 1960 decades but returned to the 1930 decade height in the 1970 hybrids. Variation among hybrids within decades for plant and ear height was significant for all decades (Table 20).

Significant increases in percentage plant emergence occurred between the 1930 and 1940 and between the 1960 and 1970 decades (Table 18). The increase in percentage emergence across decades was 5.2% (Table 18).

All plant traits displayed significant public decade x environment interactions (Table 21). Examination of decade by environment means revealed no logical interpretations of these interactions. No significant public decade x density interactions were found for plant traits (Table 22).

Dry Matter Accumulation Traits

The data for dry matter accumulation traits are given in Tables 23-31 and illustrated by Figures 9-11. Striking differences were observed among environmental means for seedling dry weight per plant and seedling dry weight yield per hectare (Table 23). The maize seedlings were harvested 45 days after planting and differences among environments may have been due in part to slow germination in dry soil conditions at Ames in 1981. Differences among environmental means for dry matter per plant and dry matter yield at both 50% silk and at harvest were significant (Table 23). Note that the relative rank of the environmental means for dry matter per plant and dry matter yield changed from the seedling stage to later growth stages. For example, greatest dry matter per seedling and least dry matter per plant at harvest both occurred at Ames in 1980.

As expected, the normal effect of plant density on dry matter accumulation was important only at later growth stages (Table 25). Significant differences in density means were found for all dry matter accumulation traits at 50% silk and at harvest (Table 25). For all dry matter accumulation traits, increasing plant density decreased dry matter per plant and increased dry matter yields.

A linear model best described the significant changes of all dry matter accumulation traits across decades (Table 26).

Table 23. Means for dry matter (DM) accumulation traits of 24 single-cross hybrids grown at three plant densities in several environments

	Seedling dry weight		Dry weight at 50% silk		Dry weight at harvest		Veg. DM per plant at harvest (g)	Harvest index grain wt. per plant (g)
	Per plant (g)	Yield (kg/ha)	Per plant (g)	Yield (mt/ha)	Per plant (g)	Yield (mt/ha)		
Ames 1980	6.92	640.2	174.2	7.24	329.0	13.25	157.7	171.3
Ames 1981	0.94	88.1	153.6	6.29	341.7	13.91	183.7	158.0
Ankeny 1980	-	-	-	-	354.7	15.35	194.2	160.5
Ankeny 1981	3.04	263.8	161.7	6.57	402.7	16.37	191.9	210.5
$LSD_{0.05}$	0.36	140.9	7.7	0.39	35.4	2.08	19.3	23.0
Density L	3.74	259.4	193.3	5.53	450.3	13.01	230.5	219.8
Density M	3.61	329.7	158.4	6.78	338.8	14.91	170.8	167.9
Density H	3.55	403.0	137.7	7.79	283.6	16.06	141.5	142.1
$LSD_{0.05}$	0.36	140.9	7.7	0.39	32.0	1.88	17.5	20.8
Overall $\bar{X}$	3.63	330.7	163.2	6.70	357.2	14.66	180.7	176.5
C.V. %	29.6	30.6	14.2	14.8	10.5	12.9	15.8	14.0

Table 24. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for dry matter (DM) accumulation traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in several environments

Decade of hybrids	Seedling dry weight		Dry wt. at 50% silk		Dry wt. at harvest		Veg. DM per plant at harvest (g)	Harvest index grain wt. per plant (g)
	Per plant (g)	Yield (kg/ha)	Per plant (g)	Yield (mt/ha)	Per plant (g)	Yield (mt/ha)		
1930	3.42	298.4	149.0	6.10	298.9	12.36	139.5	159.4
1940	3.50	321.4	159.0	6.52	332.7	13.50	157.5	175.2
1950	3.46	314.0	166.6	6.75	367.8	14.83	189.9	177.6
1960	3.83	344.6	172.5	7.01	388.2	16.00	216.0	172.2
1970	4.03	379.4	178.5	7.40	394.2	16.17	199.6	194.6
Prop 1970	3.56	326.4	153.4	6.41	362.8	15.13	182.9	179.8
$LSD_{0.05}$	0.41	36.1	8.3	0.32	12.7	0.77	9.8	8.0
b_1	0.15±0.05	18.5±4.0	7.3±0.9	0.31 ±0.04	24.6±1.4	1.01±0.06	17.9±1.1	6.7±0.9
b_q	0.05±0.04	4.4±3.4	-0.7±0.8	-0.002±0.03	-5.0±1.2	-0.15±0.05	-5.4±0.9	0.4±0.8
b_c	0.00±0.05	3.5±4.0	0.3±0.9	0.03 ±0.04	-1.6±1.4	-0.12±0.06	-5.7±1.1	4.1±0.9

Table 25. Mean squares from combined analyses of variance for dry matter accumulation traits of maize hybrids grown at three plant densities in several environments

Source	df[a]	Mean squares: Seedling dry weight: Per plant	Mean squares: Seedling dry weight: Yield	Mean squares: Dry weight: Per plant
Environment (E)	3	1989.7	17187642.9	23327.4
Reps/E	7	8.3	51825.3	891.9
Density (D)	2	2.1	1113336.3	170332.1**
D x E	6	1.3	277395.5**	547.9
Error a	14	3.9	24055.7	1711.8
Hybrid (H)	23	5.6**	60557.4**	5164.0**
H x E	69	2.2**	17412.3**	916.1**
H x D	46	0.9	12584.6**	763.8
H x D x E	138	0.8	7900.9	634.8
Error b[b]	479	1.2	10210.4	537.7

[a]Refer to Appendix Table A1 for degrees of freedom for seedling dry weight per plant, seedling dry weight yield, dry weight per plant at 50% silk, dry weight yield at 50% silk.

[b]Degrees of freedom for error b: seedling dry wt. per plant, 414; seedling dry weight yield, 414; dry weight per plant at 50% silk, 413; dry weight yield at 50% silk, 413; dry weight per plant at harvest, 478; dry weight yield at harvest, 478; vegetative dry matter per plant at harvest, 478; harvest index grain weight per plant, 479.

Mean squares				
50% silk	Dry weight at harvest		Vegetative dry matter per plant at harvest	Harvest index grain weight per plant
Yield	Per plant	Yield		
51.9	222766.2	412.4	55919.5	121810.9
1.1	6302.1	15.3	1591.5	4553.4
277.6**	1890670.9**	626.0*	539532.8**	410501.1**
2.5	22487.4**	78.0**	6731.6**	9495.0**
4.2	3881.3	12.4	1448.0	1360.1
8.3**	48264.2**	78.4**	26533.8**	8605.6**
1.4*	2690.2**	4.8*	1588.6**	1070.9**
0.9	3073.3*	5.5*	2021.2**	1112.5
1.2	1822.8*	4.0	705.5	900.6**
1.0	1406.0	3.6	819.4	609.3

Table 26. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for dry matter (DM) accumulation traits (Table 25)

Source	df	Mean squares: Seedling dry wt. Per plant	Seedling dry wt. Yield	Dry wt. at Per plant
Hybrid	23	5.6**	60557.4**	5164.0**
Decades	5	8.6**	116012.5**	18398.7**
Public decades	4	7.8*	107092.8**	14465.7**
Linear	1	25.8**	370291.5**	57049.1**
Quadratic	1	3.3	29043.9	743.3
Cubic	1	0.0	12962.7	68.0
Lack of fit	1	1.9	16073.1	2.2
1970 vs Prop 1970	1	12.0*	151691.4	34131.0**
Hybrids/decades	18	4.8*	45153.2**	1487.7
H/1930	3	7.2*	100854.9**	3090.2*
H/1940	3	2.7	49554.9*	2821.1*
H/1950	3	0.8	7088.4	881.2
H/1960	3	10.8	70083.0*	1157.7
H/1970	3	0.8	7732.8	582.6
H/Prop 1970	3	6.3*	35604.9	393.4

Mean squares				
50% silk	Dry wt. at harvest		Veg. DM per plant at harvest	Harvest index grain wt. per plant
Yield	Per plant	Yield		
8.3**	48264.2**	78.4**	26533.8**	8605.7**
31.5**	183053.1**	296.4**	107217.7**	19774.1**
26.1**	212540.5**	352.6**	129457.1**	21116.3**
103.4**	799644.8**	1350.4**	421369.1**	60073.5**
0.0	46728.7**	41.3*	53222.1**	275.2
1.1	3262.4	18.5	42801.0**	22429.4**
0.0	526.4	0.3	436.3	1687.0
53.2**	65103.1**	71.6*	18260.2*	14405.2**
1.9	10822.9**	17.9**	4121.6**	5503.3**
3.2	26524.1**	34.5**	3217.5	22592.7**
3.9	3921.6	10.9	5143.1*	723.1
1.6	15504.8**	26.7*	8304.8**	2353.7
1.9	4607.6	11.1	746.0	2113.1
0.7	9016.0*	20.2**	3649.1	2987.6*
0.1	5363.1	3.7	3669.3	2249.7

Table 27. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for dry matter (DM) accumulation traits (Table 25) of maize hybrids grown at three plant densities in several environments

Source	df[a]	Mean squares	
		Seedling dry wt.	
		Per plant	Yield
Hybrid x environment (E)	69	2.2**	17412.3**
Decades x E	15	3.4**	9669.9
Public decades x E	12	3.1**	48894.9**
Linear x E	3	7.1**	110652.3**
Quadratic x E	3	1.6	25448.0
Cubic x E	3	0.2	2354.9
Lack of fit x E	3	3.5	57124.4**
1970 vs Prop 1970 x E	3	4.5*	48349.4**
Hybrids/decades x E	54	1.9*	19563.0**
H/1930 x E	9	1.9	32962.2**
H/1940 x E	9	0.6	13110.8
H/1950 x E	9	2.7*	21692.4*
H/1960 x E	9	3.9**	44707.8**
H/1970 x E	9	0.6	4904.6
H/Prop 1970 x E	9	1.7	16421.4

[a]Refer to Appendix Table A1 for degrees of freedom for seedling dry weight per plant, seedling dry weight yield, dry weight per plant at 50% silk, dry weight yield at 50% silk.

Mean squares					
Dry wt. at 50% silk		Dry wt. at harvest		Veg. DM per plant at harvest	Harvest index grain wt. per plant
Per plant	Yield	Per plant	Yield		
916.1**	1.4*	2690.2**	4.8*	1588.6**	1070.9**
989.8	1.8	3515.8	8.7**	2567.4**	630.4
1166.8*	2.1*	3865.2**	7.3*	2611.5**	671.9
2865.4**	5.3**	4575.6*	9.7*	3077.7*	212.5
872.7	2.1	8705.5**	15.6**	4279.8**	1763.7*
535.8	0.6	1921.5	2.6	2101.5	505.4
393.4	0.6	258.3	1.2	986.9	206.0
281.9	0.5	2118.0	14.6**	2391.0*	464.4
895.6*	1.3	2460.8**	3.8	1316.7	1193.2**
1250.8*	2.0	2645.0	4.1	530.5	1444.8*
998.0	1.1	1881.4	2.1	517.2	1076.7
569.4	0.7	2688.2*	3.9	1556.8*	1293.7*
1874.7**	2.9**	3156.7*	5.9	1358.1	1883.2**
364.7	0.6	2266.4	4.0	842.0	651.6
315.9	0.9	2127.2	2.5	1547.7	809.4

Table 28. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for dry matter (DM) accumulation traits (Table 25) for maize hybrids grown at three plant densities in several environments

Source	df	Mean squares	
		Seedling dry wt.	
		Per plant	Yield
Hybrid x density (D)	46	0.9	12584.6**
Decades x D	10	0.8	22625.3**
Public decades x D	8	0.7	8997.8**
Linear x D	2	0.1	9793.8**
Quadratic x D	2	0.8	7786.4**
Cubic x D	2	1.8	18306.5**
Lack of fit x D	2	0.2	104.4
1970 vs Prop 1970 x D	2	1.0	14140.8**
Hybrids/decades x D	36	0.9	9795.6**
H/1930 x D	6	0.8	13087.8**
H/1940 x D	6	1.1	11060.9**
H/1950 x D	6	0.6	7442.9**
H/1960 x D	6	1.0	10832.7**
H/1970 x D	6	1.1	7013.0**
H/Prop 1970 x D	6	0.9	9334.8**

Mean squares					
Dry wt. at 50% silk		Dry wt. at harvest		Veg. DM per plant at harvest	Harvest index grain wt. per plant
Per plant	Yield	Per plant	Yield		
763.8	0.9	3073.3*	5.5*	2021.2**	1112.5
923.2	1.6	5416.6**	12.1**	5447.4**	731.5
614.6	1.9	4976.1**	14.5**	5450.5**	866.1
343.6	4.5*	2645.0	32.4**	9100.9**	2169.6
84.0	0.1	2983.3	0.3	2132.1	87.6
1219.8	2.0	7761.2*	15.7*	4401.0**	1198.8
811.3	1.2	6514.9*	9.7	6167.9**	8.4
2157.5*	0.1	7178.6*	2.6	5434.9**	193.2
719.5	0.7	2422.4	3.7	1069.4	1218.3
1111.7	0.1	5112.6	4.3	1301.1	2700.0**
1117.9	0.8	1441.1	3.4	627.7	1496.1
374.1	0.8	1796.6	2.9	733.4	592.5
363.0	0.5	1421.3	3.6	762.6	1500.2
324.7	0.6	2176.0	2.6	1146.1	613.5
1025.7	1.6	2587.0	5.3	1845.7*	407.4

Table 29. Environment x decade means for dry matter per seedling of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1981	Ames 1980	Range
	g			
1930	0.94	2.92	6.40	5.46
1940	0.87	2.76	6.88	6.01
1950	0.92	2.83	6.62	5.70
1960	0.90	3.01	7.57	6.67
1970	0.99	3.58	7.54	6.55
Prop 1970	1.01	3.12	6.54	5.53
$\bar{X}$	0.94	3.04	6.92	

$LSD_{0.05}$ = 0.51 g across environments within a decade

Table 30. Environment x decade means for dry matter per plant at 50% silk of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1981	Ames 1980	Range
	g			
1930	140.4	156.1	150.3	15.7
1940	152.0	155.4	169.6	17.6
1950	157.5	165.6	176.8	19.3
1960	165.3	168.0	183.9	18.6
1970	163.4	176.5	195.7	32.3
Prop 1970	142.8	148.5	168.9	26.1
$\bar{X}$	153.6	161.7	174.2	

$LSD_{0.05}$ = 10.7 g across environments within a decade

Table 31. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for dry matter accumulation traits for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrids	Density L	Density M	Density H	b_{lin}	b_{quad}
	Seedling weight per hectare (kg/ha)				
1930	241.6	310.6	342.9	50.7	-6.12
1940	239.7	318.1	406.4	83.4	1.65
1950	242.2	309.1	390.9	74.4	2.48
1960	279.5	343.9	410.4	65.5	0.35
1970	289.1	388.5	460.4	85.7	4.58
Prop 1970	264.4	307.7	407.0	71.3	9.33
$LSD_{0.05}$	17.5	17.5	17.5	29.0	16.76
	Dry matter at harvest per plant (g)				
1930	382.2	280.9	233.6	-74.3	9.00
1940	428.2	316.1	253.7	-87.3	8.28
1950	478.3	341.7	285.0	-96.7	13.32
1960	475.5	368.6	324.0	-75.8	10.38
1970	494.2	378.7	309.6	-92.3	7.73
Prop 1970	444.3	348.3	295.8	-74.3	7.25
$LSD_{0.05}$	17.8	17.8	17.8	12.6	7.29
	Dry matter at harvest per hectare (mt/ha)				
1930	11.30	12.40	13.40	1.05	-0.02
1940	12.31	13.92	14.28	0.99	-0.21
1950	13.72	14.83	15.91	1.10	-0.01
1960	13.60	16.22	18.05	2.20	-0.13
1970	14.20	16.64	17.70	1.75	-0.23
Prop 1970	12.90	15.44	17.04	2.07	-0.16
$LSD_{0.05}$	0.80	0.80	0.80	0.59	0.34
	Vegetative dry matter at harvest per plant (g)				
1930	174.0	134.3	110.1	-32.0	2.58
1940	205.2	148.8	118.3	-43.5	4.32
1950	254.5	173.6	142.4	-56.1	8.28
1960	260.9	207.8	181.2	-39.9	4.42
1970	260.7	189.5	148.5	-56.1	5.03
Prop 1970	228.9	171.8	148.1	-40.4	5.57
$LSD_{0.05}$	11.8	11.8	11.8	11.9	4.53

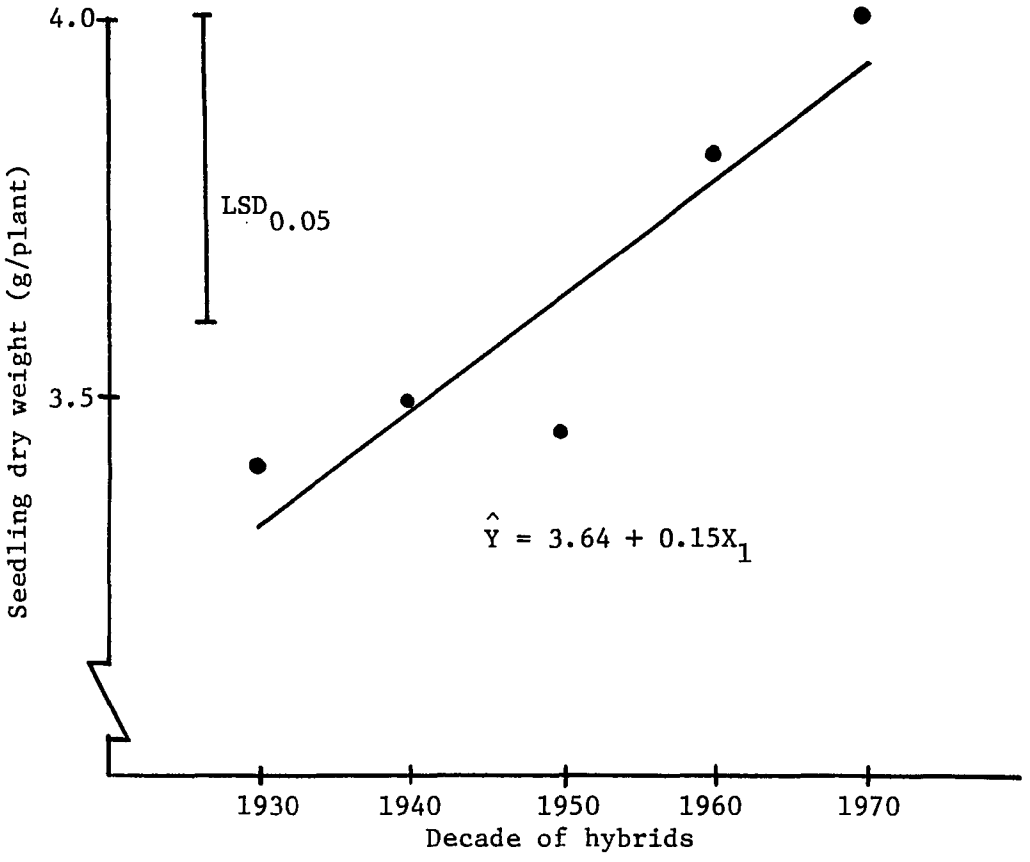

Figure 9. Predicted seedling dry weights for hybrids at 10-year intervals based on actual seedling dry weights of four public hybrids selected to represent each decade from 1930 to 1970

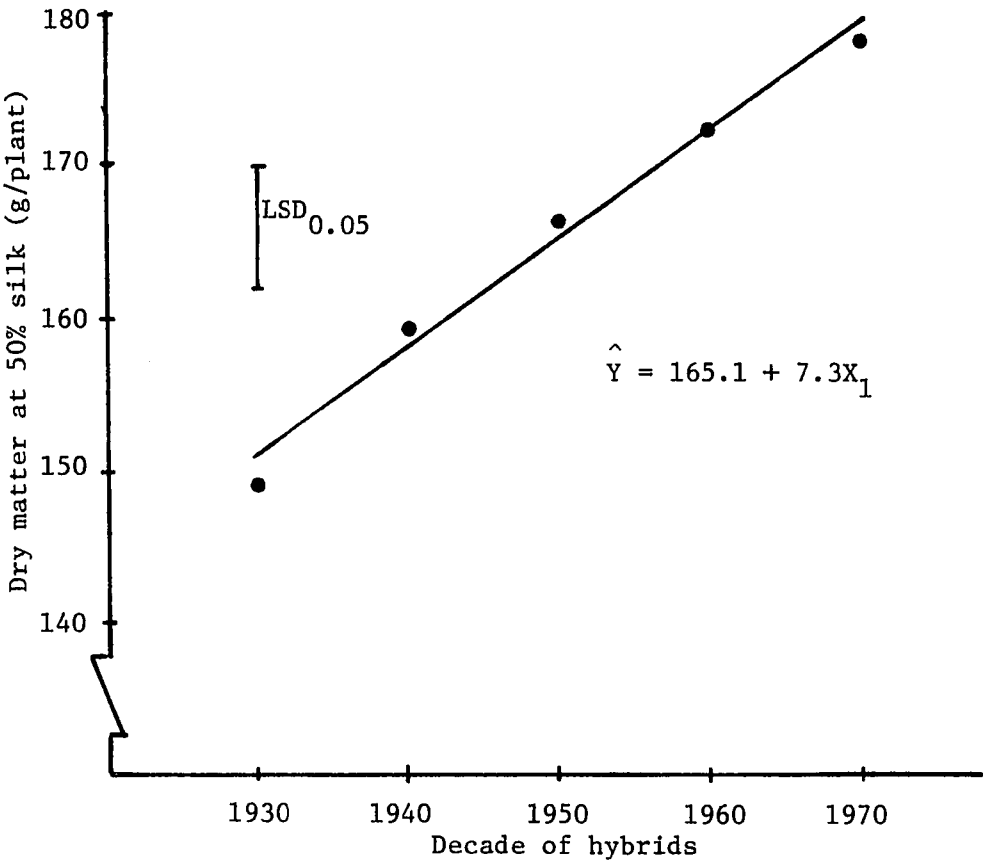

Figure 10. Predicted dry matter per plant at 50% silk for hybrids at 10-year intervals based on actual dry matter per plant at 50% silk of four public hybrids selected to represent each decade from 1930 to 1970

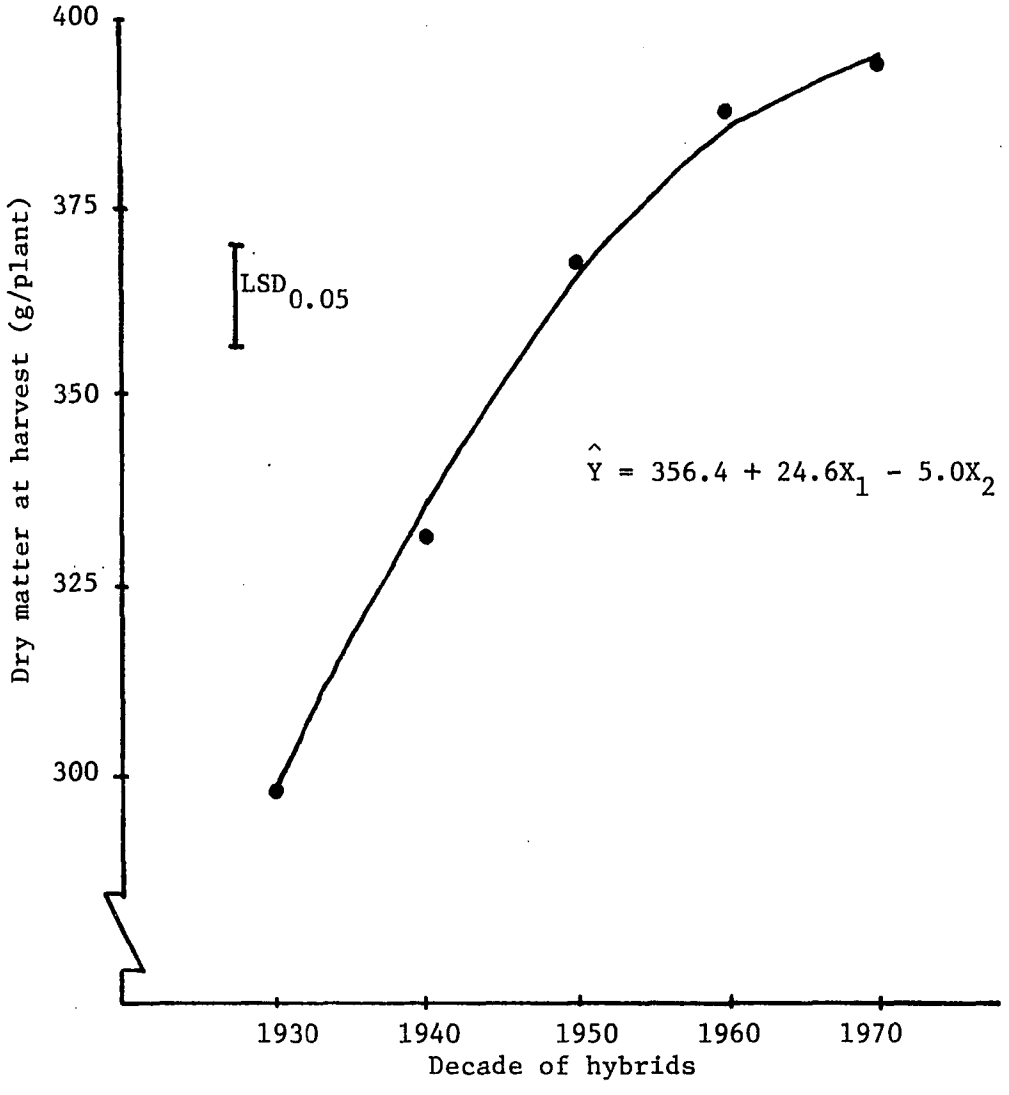

Figure 11. Predicted dry matter per plant at harvest for hybrids at 10-year intervals based on actual dry matter per plant at harvest of four public hybrids selected to represent each decade from 1930 to 1970

Figure 9 demonstrates that the linear change in seedling dry matter was 0.15 ± 0.05 g dry matter per plant per decade. Note the excellent linear fit of dry matter per plant at silking (Figure 10). Dry matter per plant at harvest increased primarily linearly between the 1930 and 1960 decades, but no significant increase occurred between the 1960 and 1970 decades which likely accounts for the significant quadratic fit (Table 26 and Figure 11). Dry matter per plant increased 0.61 g at the seedling stage, 29.5 g at silking, and 95.3 g at harvest between the 1930 and 1970 decades (Table 24). The 1970 hybrid group produced 32% more dry matter by harvest than did the 1930 group. Note that, although total dry matter per plant increased slightly between the 1960 and 1970 decades, vegetative dry matter per plant showed a significant decrease (Table 24). This indicates that 1970 hybrids partitioned relatively more dry matter to the grain. The 1970 public hybrids produced significantly more dry matter at all stages of plant growth than the 1970 proprietary hybrids (Table 24).

Public decades x environment mean squares were significant for most dry matter accumulation traits (Table 27). Although decade by environment means for dry matter per seedling were similar in the lowest yielding environment (Ames 1981), 1960 and 1970 hybrid seedlings were approximately 18% larger than hybrids of other decades in the highest yielding environment (Ames 1980) (Table 29). Data in Table 30 indicated that

1970 hybrids also were better able to take advantage of the high yielding environment for the production of dry matter prior to silking. No reasonable interpretation of the public decade x environment interactions for vegetative and total dry matter per plant at harvest could be made.

Public decades x density interactions for seedling dry weight yield, dry weight per plant at harvest, dry weight yield at harvest and vegetative dry matter per plant at harvest were significant (Table 28). Linear regression coefficients for each decade across plant densities for these traits (Table 31) indicated that modern hybrids were not more density tolerant than earlier hybrids for dry matter accumulation.

Assimilate Partitioning Traits

Assimilate partitioning traits data are given in Tables 32-38 and Figures 12-14. Significant differences among environmental means for assimilate partitioning traits were found (Table 32). Harvest indices ranged from 53.0% at Ankeny in 1981 to 45.4% at Ankeny in 1980 (Table 22). Although grain-filling duration expressed in days varied significantly between the two environments, the number of heat units representing the grain-filling period at each environment did not differ significantly. The rate of grain filling at Ames in 1980, the higher yielding environment, was significantly greater than at Ankeny 1981 (Table 32).

Table 32. Means for assimilate partitioning traits of 24 single-cross hybrids grown at three plant densities in several environments

	Harvest index %	Rate of grain filling		Grain-filling duration	
		g/heat unit	g/day	heat units	days
Ames 1980	52.3	0.3003	3.7	719.5	59.3
Ames 1981	46.3	-	-	-	-
Ankeny 1980	45.4	-	-	-	-
Ankeny 1981	53.0	0.2629	2.9	736.2	67.2
$LSD_{0.05}$	3.8	0.0158	0.7	36.5	4.2
Density L	49.0	0.3523	3.9	737.1	66.2
Density M	49.5	0.2787	2.9	727.1	65.8
Density H	50.2	0.2132	2.5	719.3	63.0
$LSD_{0.05}$	3.8	0.0193	0.9	44.7	5.2
Overall $\bar{X}$	49.6	0.2813	3.3	727.8	63.3
C.V. %	12.2	15.5	15.7	2.9	3.7

Harvest index and grain-filling duration were not affected by plant density (Table 32). Increasing plant densities, however, significantly reduced the rate of grain filling (Table 32).

The decades of hybrids differed significantly for all assimilate partitioning traits (Table 33). Harvest indices

Table 33. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for assimilate partitioning traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at the plant densities in several environments

Decade of hybrids	Harvest index %	Rate of grain filling		Grain-filling duration	
		g/heat unit	g/day	heat units	days
1930	52.7	0.266	3.2	699.8	59.1
1940	52.7	0.288	3.4	699.2	59.8
1950	48.7	0.269	3.0	743.2	66.5
1960	44.0	0.284	3.3	733.9	64.3
1970	49.7	0.312	3.6	731.0	63.7
Prop 1970	49.6	0.271	3.2	759.7	66.2
$LSD_{0.05}$	1.8	0.018	0.2	12.0	1.2
b_1	-1.5± 0.2	0.0088± 0.0020	0.07± 0.03	9.71± 1.29	1.38± 0.14
b_q	0.8± 0.2	0.0034± 0.0017	0.06± 0.02	-4.14± 1.09	-0.82± 0.12
b_c	1.4± 0.2	0.0040± 0.0020	0.06± 0.03	-3.82± 1.29	-0.42± 0.14

Table 34. Mean squares from combined analyses of variance for assimilate partitioning traits of maize hybrids grown at three plant densities in several environments

Source	df[a]	Harvest index %	Rate of grain filling		Grain-filling duration	
			g/heat unit	g/day	heat units	days
Environment (E)	1	2973.2	0.148	62.2	30077.8	6682.0
Reps/E	4	177.1	0.012	1.8	3318.9	62.0
Density (D)	2	88.7	0.695**	99.4*	11489.3	19.7
D x E	2	255.6**	0.012	3.1*	7778.3**	103.4*
Error a	8	48.5	0.004	0.5	1125.7	13.8
Hybrid (H)	23	443.6**	0.013**	1.6**	14313.5**	253.7**
H x E	23	56.1**	0.003	0.5*	1202.8**	14.2**
H x D	46	57.1*	0.003*	0.4*	712.2*	9.1*
H x D x E	46	36.1	0.001	0.2	457.7	5.2
Error b[b]	478	36.9	0.002	0.3	434.6	5.6

[a]Refer to Appendix Table A1 for degrees of freedom for harvest index.

[b]Degrees of freedom for error b: harvest index, 478; rate of grain filling, heat units, 267; rate of grain filling, days, 267; grain-filling duration, days, 276; grain-filling duration, heat units, 276.

Table 35. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for assimilate partitioning traits (Table 34)

Source	df	Mean squares				
		Harvest index %	Rate of grain filling		Grain-filling duration	
			g/heat unit	g/day	heat units	days
Hybrid	23	443.6**	0.013**	1.6**	14313.5**	253.7**
Decades	5	1342.5**	0.031**	4.2**	30182.0**	607.3**
Public decades	4	1677.6**	0.023**	3.3**	30309.8**	706.5**
Linear	1	2788.8**	0.056**	3.5*	67851.0**	1364.0**
Quadratic	1	1052.0**	0.012	4.2**	17298.0**	675.2**
Cubic	1	2757.5**	0.018*	2.8*	10494.0**	126.7**
Lack of fit	1	112.2	0.008	2.6*	25596.0**	660.1**
1970 vs Prop 1970	1	2.0	0.061**	7.6*	29671.2**	210.2**
Hybrids/decades	18	193.8**	0.007*	1.0	9905.6**	155.5**
H/1930	3	698.4**	0.022**	3.0**	26641.2**	351.4**
H/1940	3	240.6**	0.004	0.7	2107.2	37.6
H/1950	3	79.1	0.003	0.4	3377.4	46.9
H/1960	3	4.8	0.003	0.4	13410.0**	90.8**
H/1970	3	56.8	0.007	0.8	8961.6**	165.5**
H/Prop 1970	3	83.4	0.006	0.6	13876.2**	240.5**

Table 36. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for assimilate partitioning traits (Table 34) grown at three plant densities in several environments

Source	df[a]	Mean squares				
		Harvest index %	Rate of grain filling		Grain-filling duration	
			g/heat unit	g/day	heat units	days
Hybrid x environment (E)	23	56.1**	0.003	0.5*	1202.8**	14.2**
Decades x E	5	72.8*	0.006*	1.1**	669.6	3.2
Public decades x E	4	70.4*	0.007**	1.3**	596.9	3.3
Linear x E	1	47.3	0.005	0.8	227.7	0.3
Quadratic x E	1	102.0*	0.013*	2.1**	1614.6	9.4
Cubic x E	1	51.1	0.005	1.0*	177.3	3.5
Lack of fit x E	1	81.0	0.006	1.3*	368.1	0.0
1970 vs Prop 1970 x E	1	82.4	0.000	0.0	960.3	2.8
Hybrids/decades x E	18	51.4*	0.003	0.3	1350.9**	17.3**
H/1930 x E	3	35.3	0.004	0.6	1241.7*	12.3
H/1940 x E	3	31.2	0.001	0.1	3213.3**	45.0**
H/1950 x E	3	82.9*	0.001	0.0	812.4	13.0
H/1960 x E	3	72.3*	0.001	0.1	1429.2*	4.9
H/1970 x E	3	18.8	0.007*	0.7*	1067.4	22.4**
H/Prop 1970 x E	3	67.9	0.003	0.3	341.1	6.2

[a]Refer to Appendix Table A1 for degrees of freedom for harvest index.

Table 37. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for assimilate partitioning traits (Table 34) grown at three plant densities in several environments

Source	df	Mean squares				
		Harvest index	Rate of grain filling		Grain-filling duration	
		%	g/heat unit	g/day	heat units	days
Hybrid x density (D)	46	57.1*	0.003*	0.4*	712.2*	9.1*
Decades x D	10	102.9**	0.005**	0.9**	477.4	7.1
Public decades x D	8	100.3**	0.007**	1.0**	586.4	8.6
Linear x D	2	130.1*	0.020**	2.9**	1774.2*	23.6*
Quadratic x D	2	14.3	0.001	0.4	139.8	7.0
Cubic x D	2	161.4*	0.002	0.2	424.8	2.8
Lack of fit x D	2	95.4	0.004	0.6	6.9	1.1
1970 vs Prop 1970 x D	2	113.1*	0.000	0.1	41.4	1.2
Hybrids/decades x D	36	44.4	0.002	0.3	777.4*	9.7*
H/1930 x D	6	62.1	0.002	0.3	2221.1**	23.6**
H/1940 x D	6	70.5	0.004	0.4	304.6	5.3
H/1950 x D	6	19.0	0.002	0.2	238.0	3.9
H/1960 x D	6	56.4	0.001	0.2	554.6	9.5
H/1970 x D	6	20.3	0.002	0.2	575.9	6.7
H/Prop 1970 x D	6	38.2	0.001	0.2	770.0	8.9

Table 38. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for assimilate partitioning traits for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrids	Density L	Density M	Density H	b_{lin}	b_{quad}
		Harvest index (%)			
1930	54.0	51.6	52.3	-0.85	0.52
1940	52.1	52.6	53.4	0.65	0.05
1950	46.9	49.5	49.8	1.45	-0.38
1960	45.1	42.8	44.2	-0.45	0.62
1970	47.4	49.7	52.1	2.50	0.02
Prop 1970	48.6	50.8	49.3	0.35	-0.62
$LSD_{0.05}$	2.5	2.5	2.5	1.9	1.07
		Rate of grain filling (g/heat unit)			
1930	0.3614	0.2511	0.1903	-0.0856	0.0083
1940	0.3761	0.2815	0.2007	-0.0877	0.0023
1950	0.3290	0.2648	0.2136	-0.0577	0.0022
1960	0.3456	0.2857	0.2211	-0.0623	-0.0008
1970	0.3686	0.3185	0.2482	-0.0602	-0.0034
Prop 1970	0.3334	0.2736	0.2053	-0.0641	-0.0014
$LSD_{0.05}$	0.0253	0.0253	0.0253	-0.0178	0.0097
		Rate of grain filling (g/day)			
1930	3.9	2.5	2.3	-0.8	0.2
1940	4.2	3.0	2.4	-0.9	0.1
1950	3.5	2.7	2.4	-0.6	0.1
1960	3.9	2.8	2.5	-0.7	0.1
1970	4.1	3.3	2.8	-0.7	0.1
Prop 1970	3.7	2.8	2.4	-0.7	0.1
$LSD_{0.05}$	0.3	0.3	0.3	0.2	0.1
		Duration of grain filling (heat unit)			
1930	716.6	697.6	685.3	-15.7	1.1
1940	709.4	702.8	685.6	-11.9	-1.8
1950	753.0	743.7	733.0	-10.0	-0.2
1960	744.6	730.5	726.7	-9.0	1.7
1970	736.1	728.6	728.3	-3.9	1.2
Prop 1970	763.0	759.3	756.9	-3.05	0.2
$LSD_{0.05}$	11.8	11.8	11.8	8.3	4.8

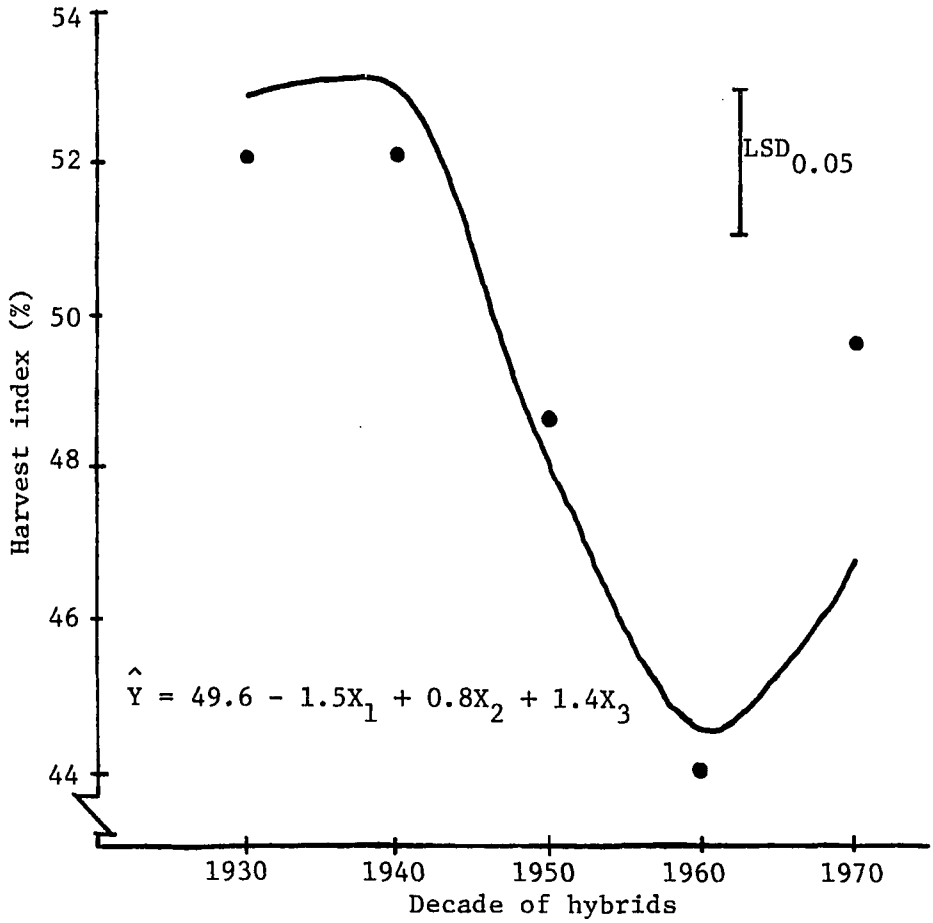

Figure 12. Predicted harvest indices for hybrids at 10-year intervals based on actual harvest indices of four public hybrids selected to represent each decade from 1930 to 1970

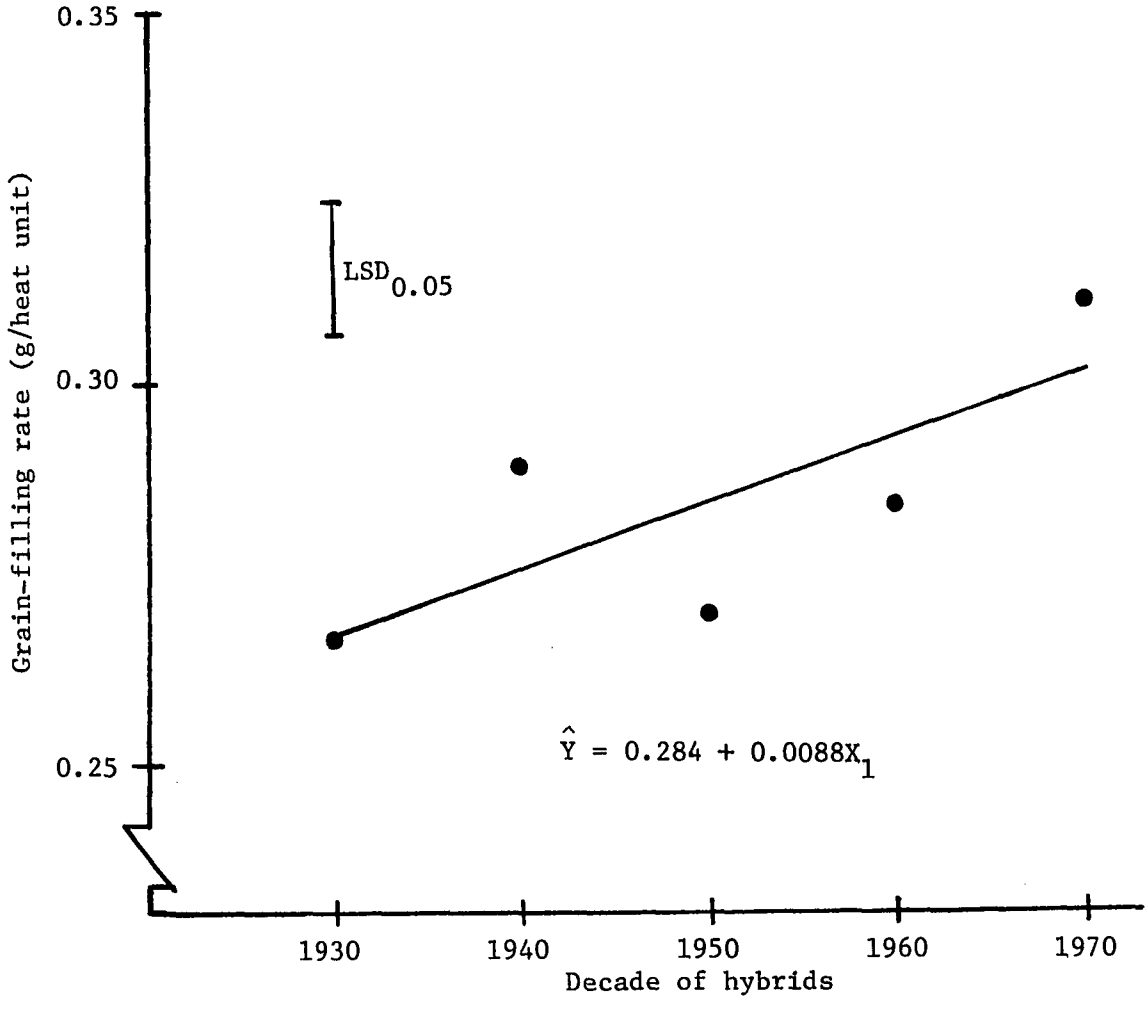

Figure 13. Predicted rates of grain filling for hybrids at 10-year intervals based on actual rates of grain filling of four public hybrids selected to represent each decade from 1930 to 1970

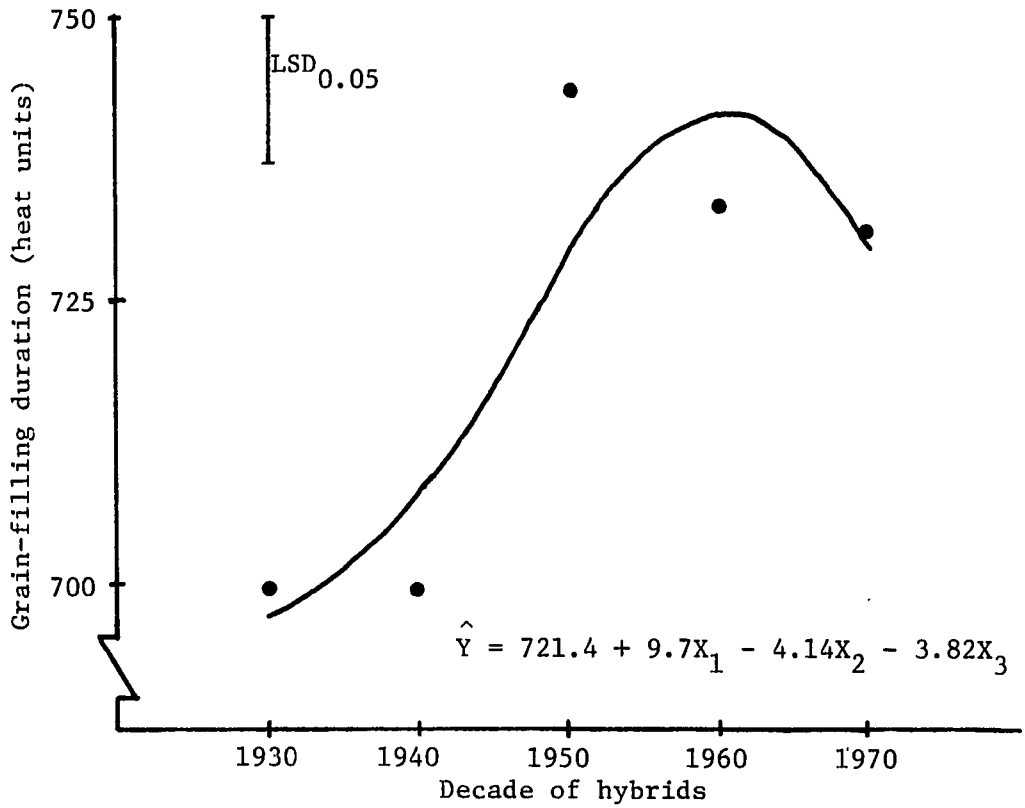

Figure 14. Predicted grain-filling durations for hybrids at 10-year intervals based on actual grain-filling durations of four public hybrids selected to represent each decade from 1930 to 1970

ranged from 52.7 to 44.0% for the 1930 and 1960 decades, respectively (Table 33). Both linear and cubic regression models described the change in harvest indices across decades equally well (Table 35). The pattern of linear decrease in harvest indices between the 1940 and 1960 decades was followed by an important increase in harvest index by the 1970 hybrids (Figure 12). Most of the variation among rate of grain filling (heat units) means was explained by a linear model (Table 35, Figure 13). Rate of grain filling (heat units) increased 0.046 g/heat unit between the 1930 and 1970 decades (Table 33). The change in rate of grain filling (days) across decades was erratic. The difference in grain-filling duration between the 1930 and 1970 decades was 4.6 days and 31.2 heat units (Table 22). Linear increases of 9.71 ± 1.29 heat units per decade or 1.38 ± 0.14 days per decade best described the change in grain-filling duration across decades (Table 33, Figure 14). Mean squares for all regression models for grain-filling duration, however, were significant (Table 35) and this was due partly to the fact that the 1950 hybrids had the longest grain-filling duration and that no significant changes in grain-filling duration occurred between the 1930 and 1940 and the 1960 and 1970 decades (Table 33 and Figure 14). The number of heat units per day varied widely between the beginning and the end of the grain-filling period. Comparison between the grain-filling-duration-decade means given in heat units

and days (Table 33) indicates that measurement in days exaggerates differences among decades.

The 1970 proprietary hybrids displayed a significantly longer grain-filling duration, i.e., 2.5 days and 28.7 heat units, than the 1970 public hybrids (Table 33). Harvest indices in 1970 public and proprietary hybrids were similar. The rate of grain filling, however, was significantly higher in 1970 public hybrids than in their proprietary counterparts (Table 33).

The public decades x environment interactions were significant for harvest index and rate of grain filling (Table 36). No logical interpretations of these interactions were possible.

The relative performance of the decades of hybrids for assimilate partitioning traits depended upon plant density (Table 37). The linear responses of harvest indices to increased plant densities were b = -0.85% for the 1930 decade and b = 2.50% for the 1970 decade (Table 38). Although the 1970 hybrids' positive linear response to increased plant density indicated density tolerance for harvest index, this was not true of the 1960 hybrids (Table 38). Increasing plant densities decreased the rate of grain filling and the grain-filling duration in all decades (Table 38). The magnitude of the negative response of grain-filling duration to increased

plant density was significantly smaller, however, in the 1970 decade, indicating a greater density tolerance (Table 38).

Source Traits

Data for source traits are given in Tables 39-47 and illustrated by Figures 15-17. The expressions of plant leaf area, leaf orientation values (LOV) both above and below the ear, and leaf senescence were significantly affected by environment (Table 39). Percentages of plants with tillers, at the Ankeny environments, were approximately twice those at the Ames environments. The fact that plants at the Ankeny environments were more mature when thinned and tillers were not confused with extra plants may explain these observed differences. Environmental means for carbon dioxide exchange rate (CER), leaf area index (LAI), and spring vigor did not differ significantly (Table 39).

Plant density effects on plant leaf area, LAI, spring vigor, and percentage plants with tillers were significant (Table 39). One would logically expect plant density to affect LAI, percentage plants with tillers, and spring vigor rating. As plant densities increased, leaf area per plant decreased 5.8 cm^2 (Table 43).

Mean squares for CER (Table 42) indicated that differences among decades were not significant. Although differences among decade means for LAI were not significant, differences among

Table 39. Means for source traits of 24 single-cross hybrids grown at three plant densities in several environments[a]

	CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers (%)
Ames 1980	40.4	71.5	3.1	33.2	32.7	6.5	4.8	5.6
Ames 1981	38.7	74.0	3.1	38.2	29.2	6.6	3.6	5.0
Ankeny 1980	-	69.1	3.1	27.9	30.8	6.6	-	11.2
Ankeny 1981	-	69.1	2.9	27.6	28.8	6.8	4.1	10.0
$LSD_{0.05}$	3.1	3.2	0.4	3.7	3.1	0.3	0.8	2.2
Density L	40.6	73.5	2.1	32.1	30.3	6.4	3.9	12.4
Density M	40.1	71.8	3.2	32.8	31.2	6.5	4.4	6.6
Density H	38.1	67.7	3.9	30.8	30.4	6.9	4.3	4.9
$LSD_{0.05}$	3.8	2.6	0.3	3.0	2.5	0.3	0.8	1.9
Overall $\bar{X}$	39.6	71.0	3.1	31.9	30.6	6.6	4.2	8.0
C.V. %	6.5	6.3	9.2	14.2	11.0	11.3	21.1	121.2

[a]In Tables 39 through 44, CER = carbon dioxide exchange rate, mg $CO_2 dm^{-2} hr^{-1}$; PLA = plant leaf area, cm^2; LAI = leaf area index; LOVA = leaf orientation value above the ear; and LOVB = leaf orientation value below the ear.

Table 40. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for source traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in several environments

Decade of hybrids	CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers (%)
1930	40.1	68.2	3.0	27.3	30.2	6.5	1.8	25.1
1940	38.8	71.7	3.1	26.4	28.2	6.4	2.7	5.0
1950	39.9	75.6	3.2	25.7	28.3	6.5	4.8	5.0
1960	40.5	70.4	3.0	30.4	32.6	6.6	6.8	5.2
1970	37.0	71.2	3.1	43.0	32.2	7.0	4.4	3.0
Prop 1970	41.1	68.9	3.2	38.1	32.2	6.6	4.7	4.7
$LSD_{0.05}$	3.4	2.7	0.2	1.7	1.1	0.2	0.9	7.4
b_1	-0.44± 0.20	0.5± 0.2	0.01± 0.01	3.5± 0.2	0.8± 0.1	0.12± 0.02	0.92± 0.06	-4.4± 0.8
b_q	-0.35± 0.17	-1.0± 0.2	-0.03± 0.01	2.3± 0.2	0.5± 0.1	0.08± 0.02	-0.47± 0.05	2.6± 0.7
b_c	-0.65± 0.20	0.6± 0.2	0.02± 0.01	0.8± 0.2	0.7± 0.1	0.02± 0.02	-0.56± 0.06	-2.3± 0.8

Table 41. Mean squares from combined analyses of variance for source traits of maize hybrids grown at three plant densities in several environments

Source	df[a]	Mean squares							
		CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers
Environment (E)	3	313.5	777.7	1.45	3690.5	565.4	2.7	73.8	2065.9
Reps/E	5	1489.3	235.3	0.59	868.2	423.1	10.9	2.9	129.7
Density (D)	2	235.8	1870.0*	161.65**	228.8	51.2	18.3**	16.1	4521.2**
D x E	6	491.4	274.1	1.53*	129.5	106.5	2.2	10.1*	184.5
Error a	10	133.5	98.5	0.42	267.1	178.2	2.6	2.8	105.8
Hybrid (H)	23	140.6**	387.7**	0.62**	1609.4**	170.0**	7.6**	80.4**	9593.0**
H x E	69	30.2	42.5	0.21**	37.3**	16.1	0.7	3.4**	991.1**
H x D	46	25.6	23.8	0.08	29.3*	11.4	0.6	1.6*	725.4
H x D x E	138	18.1	22.2	0.07	21.9	14.7	0.4	1.0	90.7
Error b[b]	552	31.5	19.9	0.07	20.4	11.4	0.6	0.8	93.0

[a]Refer to Appendix Table A1 for degrees of freedom for CER, spring vigor rating, stay green rating and plants with tillers.

[b]Degrees of freedom for error b: plant leaf area, 343; leaf area index, 343, LOV above ear, 342, LOV below ear, 342; carbon dioxide exchange rate, 268, spring vigor rating, 552, stay green rating, 414; plants with tillers, 551.

Table 42. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for source traits (Table 41)

Source	df	Mean squares CER	PLA
Hybrid	23	140.6**	387.7**
Decades	5	234.2	677.6**
Public decades	4	142.4	777.6**
Linear	1	140.0	235.7
Quadratic	1	122.9	1609.7**
Cubic	1	305.8	333.2
Lack of fit	1	0.9	931.8**
1970 vs Prop 1970	1	601.4*	277.6
Hybrids/decades	18	114.5**	307.2**
H/1930	3	75.6**	76.5
H/1940	3	48.1*	770.7**
H/1950	3	221.6**	443.3**
H/1960	3	164.4**	273.7**
H/1970	3	166.2**	38.4
H/Prop 1970	3	11.3	240.8**

Mean squares					
LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers
0.62**	1609.4**	170.0**	7.6**	80.2**	9593.0**
0.51	4714.7**	376.9**	9.5**	319.5**	9907.0**
0.62	5570.3**	471.2**	8.8**	398.4**	12339.6**
0.10	13469.2**	737.1**	22.7**	912.9**	27907.2**
1.05	8131.6**	433.9**	11.9**	334.3**	13491.7**
0.35	671.5**	511.4**	0.4	334.3**	7335.4**
0.99	8.9	202.2**	0.4	12.2	624.2
0.08	1292.5**	0.0	12.2**	4.1	176.7
0.65**	746.8**	112.6**	7.1**	13.7**	9505.8**
0.40	304.9**	105.6**	9.8**	21.9**	56115.5**
1.78**	48.4	63.2*	3.9**	5.1	45.1
0.77*	570.5**	190.4**	2.2*	10.9*	114.4
0.33	153.4**	40.0	10.0**	4.3	610.8**
0.07	2861.2**	85.7**	0.8	29.3**	39.7
0.56	542.3**	190.7**	11.8**	10.4	109.3

Table 43. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for source traits of maize hybrids (Table 41) grown at three plant densities in several environments

Source	df[a]	Mean squares							
		CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers
Hybrid x environment (E)	69	30.2	42.5**	0.21**	37.3**	16.1	0.7	3.4**	991.1**
Decade x E	15	84.8**	87.0**	0.43**	33.7	14.1	0.6	7.8**	886.7**
Public decades x E	12	77.8*	92.6**	0.46**	37.7	14.3	0.6	7.4**	1091.1**
Linear x E	3	227.6**	156.4**	0.79**	57.7*	13.5	0.4	9.7**	2280.8**
Quadratic x E	3	60.9	115.2**	0.62**	58.5*	9.3	1.1	9.8**	1328.3**
Cubic x E	3	4.8	62.2*	0.31**	7.2	13.0	0.2	9.9**	637.4**
Lack of fit x E	3	18.0	36.6	0.12	27.5	21.5	0.8	0.5	117.8
1970 vs Prop 1970 x E	3	112.8*	64.8*	0.30**	17.7	13.4	0.7	9.2**	69.2
Hybrids/decades x E	54	15.0	30.2*	0.14**	38.3**	16.7*	0.7	2.2**	1020.1**
H/1930 x E	9	18.0	69.8**	0.46**	32.4	20.2	0.6	1.0	5671.9**
H/1940 x E	9	20.9	17.6	0.03	47.8*	6.6	1.2*	0.7	73.7
H/1950 x E	9	4.8	15.2	0.09	10.1	5.3	0.7	2.1**	51.8
H/1960 x E	9	3.9	19.6	0.02	33.1	18.8	0.6	3.0**	66.5
H/1970 x E	9	18.3	37.6	0.07	44.1*	23.2*	0.9	1.6	36.3
H/Prop 1970 x E	9	24.3	21.1	0.18**	62.1**	25.9*	0.5	4.9**	36.5

[a]Refer to Appendix Table A1 for degrees of freedom for CER and stay green rating.

Table 44. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for source traits of maize hybrids (Table 41) grown at three plant densities in several environments

Source	df	Mean squares							
		CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers
Hybrid x density (D)	46	25.6	23.8	0.08	29.3*	11.4	0.6	1.6*	725.4
Decades x D	10	31.9	13.6	0.05	65.6**	13.2	0.2	3.5**	731.4
Public decades x D	8	27.1	12.3	0.06	51.1*	15.8	0.2	3.9**	909.2
Linear x D	2	64.2	0.2	0.12	133.3**	6.0	0.1	8.6**	2275.7*
Quadratic x D	2	25.4	4.8	0.03	19.6	14.7	0.5	3.9*	630.6
Cubic x D	2	4.2	1.7	0.07	24.9	10.1	0.1	2.2	610.3
Lack of fit x D	2	14.7	42.6	0.01	26.7	32.3	0.1	0.8	120.2
1970 vs Prop 1970 x D	2	50.8	18.5	0.03	123.3**	3.0	0.0	2.0	20.0
Hybrids/decades x D	36	23.9	26.6	0.09	19.3	10.9	0.8	1.1	723.8
H/1930 x D	6	51.2	66.6**	0.11	8.4	3.6	0.5	0.1	3839.2**
H/1940 x D	6	25.9	42.6	0.18*	40.6	11.6	0.4	1.2	41.0
H/1950 x D	6	12.4	21.2	0.12	17.7	4.5	1.0	0.8	72.3
H/1960 x D	6	17.3	12.8	0.07	12.6	14.4	0.2	0.6	281.1
H/1970 x D	6	16.0	12.4	0.03	28.9	25.7	0.7	2.6*	24.1
H/Prop 1970 x D	6	20.6	4.1	0.05	7.2	5.6	1.8**	1.5	85.1

Table 45. Environment x decade means for stay green rating of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1981	Ames 1980	Range
1930	1.6	1.8	2.1	0.5
1940	2.6	2.7	2.8	0.2
1950	4.0	5.0	5.4	1.4
1960	5.8	7.0	7.6	1.8
1970	4.2	3.7	5.3	1.6
Prop 1970	3.7	4.6	5.8	2.1
$\bar{X}$	3.6	4.1	4.8	

$LSD_{0.05}$ = 0.4 across environments within a decade

Table 46. Environment x decade means for plant leaf area of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
	cm^2				
1930	67.3	69.3	65.3	70.0	4.7
1940	76.3	68.9	68.9	72.3	7.4
1950	79.7	71.8	75.4	75.4	7.9
1960	74.3	68.5	68.2	70.6	6.1
1970	75.2	68.5	70.7	70.7	6.7
Prop 1970	71.0	67.7	66.1	70.2	4.9
$\bar{X}$	74.0	69.1	69.1	71.5	

$LSD_{0.05}$ = 2.7 cm^2 across environments within a decade

Table 47. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for source traits for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrid	Density			b_{lin}	b_{quad}
	L	M	H		
		LOVA			
1930	28.7	27.8	25.4	-1.7	-0.3
1940	27.9	26.3	25.1	-1.4	0.1
1950	24.9	27.6	24.7	-0.1	-0.9
1960	29.6	31.6	29.8	0.1	-0.6
1970	42.2	43.4	43.5	0.7	-0.2
Prop 1970	39.0	39.9	35.6	-1.7	-0.9
$LSD_{0.05}$	2.1	2.1	2.1	1.5	0.9
		Stay green			
1930	1.8	1.8	1.9	0.1	0.02
1940	2.5	2.9	2.7	0.1	0.10
1950	4.7	5.0	4.7	0.0	0.10
1960	6.5	7.3	6.5	0.0	-0.27
1970	3.6	4.8	4.8	0.6	-0.20
Prop 1970	4.3	4.9	4.9	0.3	-0.10
$LSD_{0.05}$	0.5	0.5	0.5	0.3	0.18

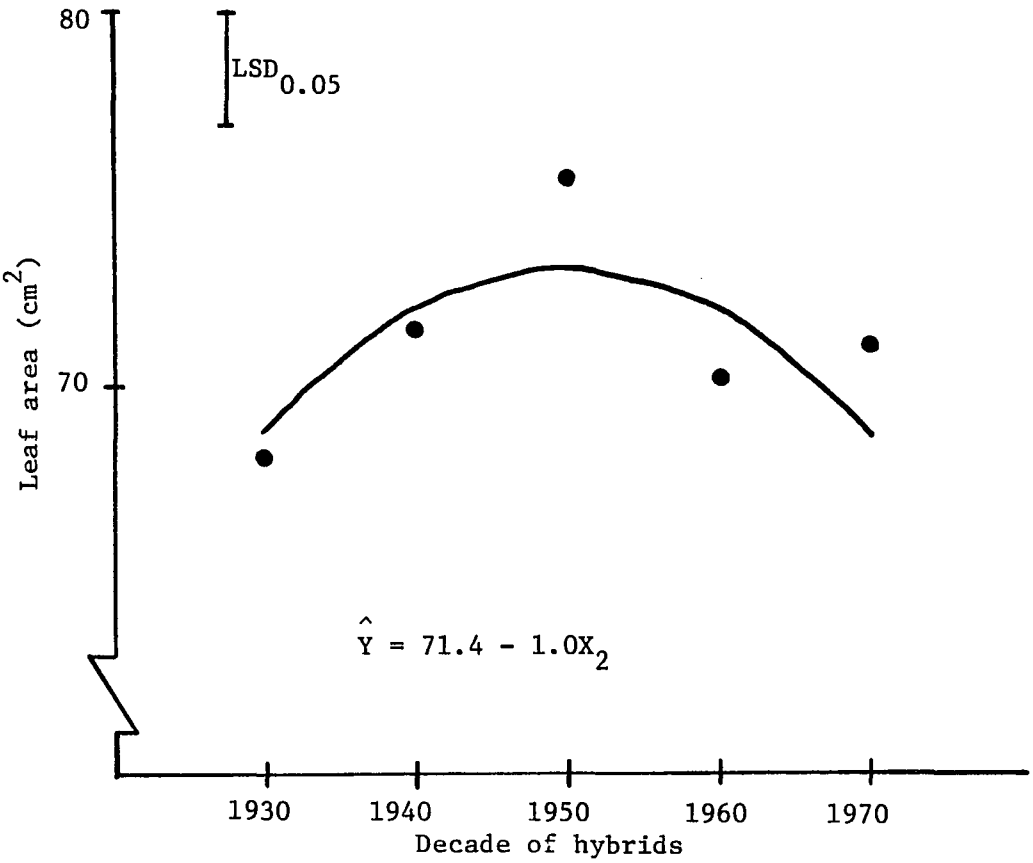

Figure 15. Predicted leaf areas per plant for hybrids based on actual leaf areas per plant of four public hybrids selected to represent each decade from 1930 to 1970

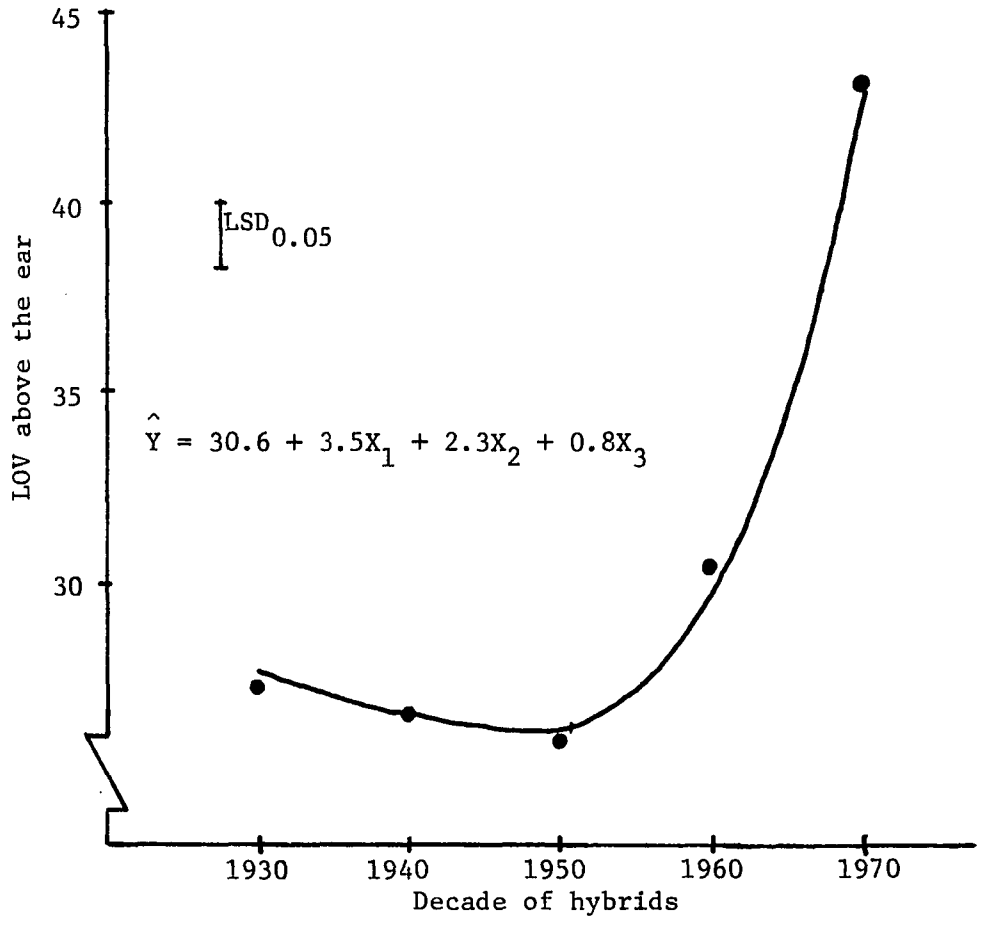

Figure 16. Predicted leaf orientation values (LOV) above the ear for hybrids based on actual LOVs above the ear of four public hybrids selected to represent each decade from 1930 to 1970

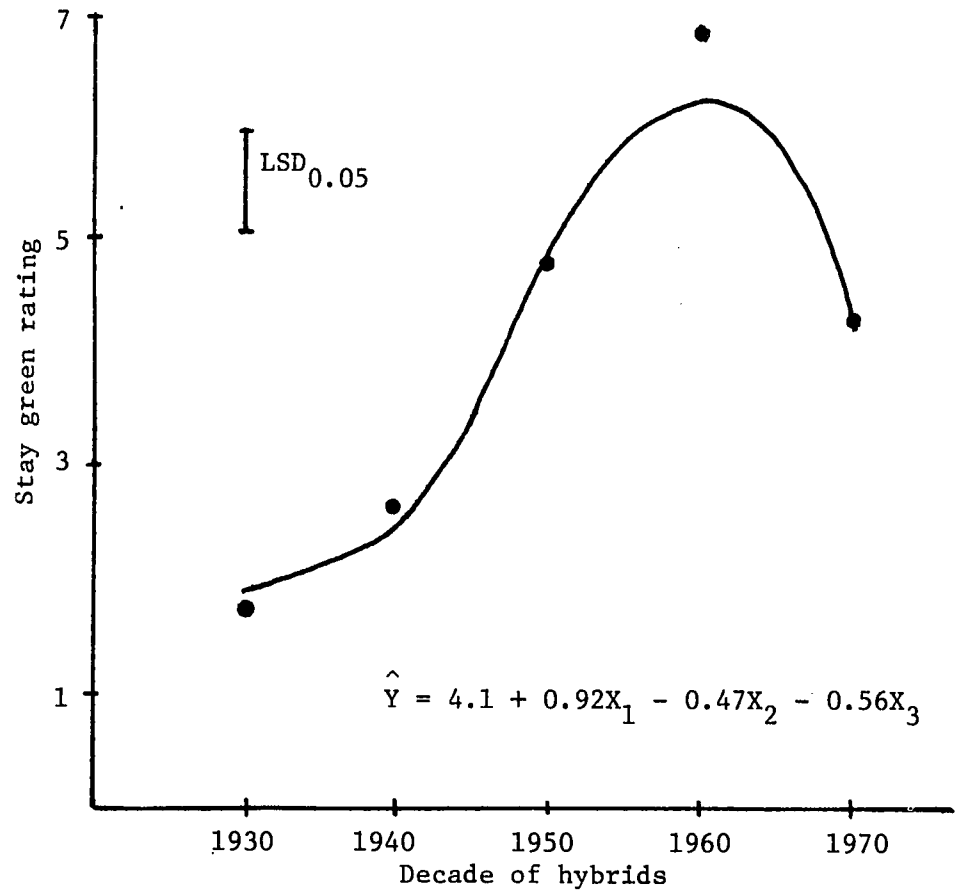

Figure 17. Predicted stay green ratings for hybrids based on actual stay green ratings of four public hybrids selected to represent each decade from 1930 to 1970

public decades for leaf area per plant were highly significant (Table 42). The change in plant leaf area across decades was best described quadratically (Table 42), as leaf area per plant increased between the 1930 to 1950 decades and decreased between the 1950 to 1970 decades (Figure 15). Leaf orientation of upper and lower canopies of hybrids became more erect across decades (Table 40). The difference in LOV below the ear between the 1930 and 1970 decades was only 2.0. Changes in leaf canopy above the ear were more pronounced, however, with LOVs of 27.3 and 43.0 for the 1930 and 1970 decades, respectively (Table 40). All of the increase in above ear leaf erectness occurred between the 1950 and 1970 decades and thus the change in LOV above the ear showed significant linear and quadratic fits (Table 42, Figure 16). The 1970 hybrids' rating for spring vigor was significantly higher than older hybrids, but the differences were very small. Stay green ratings also increased significantly across decades from 1.8 for the 1930 decade to 6.8 for the 1960 decade (Table 40). The decrease between the 1960 and 1970 decades was small but significant. The linear model accounted for most of the sums of squares for stay green rating but the quadratic and cubic model mean squares were also significant (Table 42 and Figure 17). Percentage tillering decreased dramatically from 25.1 to 5.0% between the 1930 and 1940 decades with no significant decrease thereafter (Table 40).

The 1970 public hybrids differed from 1970 proprietary

hybrids for source traits with a significantly higher LOV above the ear and spring vigor rating (Table 40).

The relative ranking of the decades of public hybrids changed significantly across environments for CER, plant leaf area, LAI, stay green rating, and percentage tillers (Table 43). Examination of the decade by environment means for stay green rating (Table 45) indicated that the 1950, 1960, and 1970 hybrids responded differentially to environments while the 1930 and 1940 hybrids did not. The highest stay green rating means for all decades were associated with the highest yielding environment, i.e., Ames 1980. No meaningful interpretation could be made of the decade by environment means for plant leaf area, LAI, and percentage plants with tillers. Note, however, that all decades, with the exception of the 1930 decade, produced their largest leaf area in the lowest yielding environment, i.e., Ames 1981 (Table 46).

Public decades x density interactions were significant only for LOV above the ear and stay green rating (Table 44). Data in Table 47 indicated a negative response of LOV above the ear with increasing plant density for the 1930, 1940, and 1950 decades, whereas positive responses were exhibited by 1960 and 1970 decades. The small increases in stay green rating across densities were nonsignificant except for the 1970 decade (Table 47) and likely were due to the difficulty of making comparable ratings at different plant densities.

Ear-Sink Traits

The data for ear-sink traits are given in Tables 48-58 and are illustrated by Figures 18-24. The effect of environment on kernel traits was significant (Table 48). Kernel number per plant was significantly greater at Ames in 1980, i.e., 723.2 kernels per plant, than at any other of the three environments, which were not significantly different from each other (Table 48). Both total and machine-harvestable ears per plant were significantly affected by environment with ranges of 0.09 and 0.13, respectively (Table 48). Ear length, however, remained constant over environments (Table 48).

Plant density affected all ear-sink traits except kernel weight (Table 48). The general effect of increasing plant density was to decrease the size of the ear-sink trait.

In general, determinants of ear-sink size increased significantly across decades (Table 49). The changes in ear-sink traits across decades were primarily linear except for ear length and kernel number which were quadratic and cubic, respectively (Table 51). The 1950 hybrids had the longest ears (20.5 cm) and the range among decade means was 2.1 cm (Table 49). The linear increase of 0.077 ± 0.006 machine-harvestable ears per plant per decade was almost three times larger than the comparable linear rate of increase in total ears per plant, i.e., b = 0.027 ± 0.004 (Table 49, Figures 18 and 19). Except for the 1940 decade mean for kernel number,

Table 48. Means for ear-sink traits of 24 single-cross maize hybrids grown at three plant densities in four environments

	Ear length (cm)	Kernel depth (mm)	Kernel weight (g)	Kernel number/ plant	Total ears/ plant	MH ears/ plant
Ames 1980	19.1	9.8	0.30	723.2	0.96	0.91
Ames 1981	19.3	9.3	0.33	505.3	0.88	0.78
Ankeny 1980	18.9	9.3	0.29	558.4	0.90	0.88
Ankeny 1981	20.3	10.2	0.35	571.2	0.97	0.86
$LSD_{0.05}$	1.3	0.3	0.02	87.0	0.08	0.09
Density L	21.7	10.4	0.33	750.8	1.01	0.96
Density M	19.1	9.5	0.32	571.5	0.93	0.85
Density H	17.7	9.2	0.32	453.8	0.84	0.76
$LSD_{0.05}$	1.2	0.3	0.02	78.7	0.07	0.08
Overall $\bar{X}$	19.5	9.7	0.32	591.0	0.93	0.85
C.V. %	8.2	10.8	33.0	18.4	10.7	12.9

Table 49. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for ear-sink traits of four public single-cross hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in four environments

Decade of hybrids	Ear length (cm)	Kernel depth (mm)	Kernel weight (g)	Kernel number/ plant	Total ears/ plant	MH ears/ plant
1930	18.4	9.01	0.306	522.7	0.84	0.63
1940	19.5	9.91	0.292	639.8	0.93	0.79
1950	20.5	9.49	0.323	574.2	0.93	0.89
1960	19.8	9.74	0.325	580.5	0.94	0.93
1970	19.5	10.01	0.354	646.6	0.97	0.94
Prop 1970	19.1	9.93	0.324	584.6	0.95	0.94
$LSD_{0.05}$	0.5	0.36	0.026	43.5	0.05	0.03
b_1	0.3± 0.1	0.18± 0.04	0.013± 0.002	18.9± 4.9	0.027± 0.004	0.077± 0.006
b_q	-0.3± 0.1	-0.04± 0.03	0.004± 0.002	-2.2± 4.1	-0.007± 0.003	-0.026± 0.005
b_c	0.1± 0.1	0.13± 0.04	-0.002± 0.002	24.2± 4.9	0.011± 0.004	0.004± 0.006

Table 50. Mean squares from combined analyses of variance for ear-sink traits of maize hybrids grown at three plant densities in four environments

Source	df	Mean squares					
		Ear length	Kernel depth	Kernel weight	Kernel number/ plant	Total ears/ plant	MH ears/ plant
Environment (E)	3	80.1	41.3	0.15	1803432	0.40	0.72
Reps/E	7	7.9	5.6	0.01	79763	0.02	0.01
Density (D)	2	1094.7**	108.7**	0.02	5806660**	1.91**	2.71**
D x E	6	31.4**	4.3	0.02	136113**	0.13**	0.12*
Error a	14	3.7	1.6	0.01	12224	0.03	0.03
Hybrid (H)	23	44.4**	15.5**	0.04**	210023**	0.10**	0.51**
H x E	69	3.9**	2.2**	0.01	31562**	0.02**	0.05**
H x D	46	3.1	3.2**	0.01	18621*	0.02**	0.02**
H x D x E	138	3.2	1.6**	0.01	10255	0.01	0.01
Error b[a]	482	2.6	1.1	0.01	11786	0.01	0.01

[a]Degrees of freedom for error b: ear length, 479; kernel depth, 479; kernel weight, 478; kernel number, 465; total ears/plant, 482; harvestable ears/plant, 482.

Table 51. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for ear-sink traits (Table 50)

Source	df	Mean squares					
		Ear length	Kernel depth	Kernel weight	Kernel number/ plant	Total ears/ plant	MH ears/ plant
Hybrid	23	44.4**	15.5**	0.04**	210023**	0.10**	0.51**
Decades	5	62.3**	16.9**	0.07**	328155**	0.26**	1.83**
Public decades	4	74.7**	21.0**	0.07**	346852**	0.32**	2.29**
Linear	1	87.8**	44.2**	0.22**	469114**	0.98**	7.88**
Quadratic	1	183.8**	3.3	0.03	8593	0.11	1.24**
Cubic	1	4.0	23.4**	0.00	775962**	0.17	0.02
Lack of fit	1	23.1*	13.2*	0.03	133742*	0.03	0.00
1970 vs Prop 1970	1	12.9	0.3	0.06*	253367**	0.02	0.00
Hybrids/decades	18	39.4**	15.2**	0.03**	177208**	0.05**	0.15
H/1930	3	77.3**	51.8**	0.01	191153**	0.08*	0.55
H/1940	3	34.3**	10.3**	0.03**	110355*	0.09*	0.13
H/1950	3	12.4*	6.9*	0.01	75135	0.05	0.09
H/1960	3	27.4*	5.0	0.05**	130471**	0.01	0.01
H/1970	3	25.2**	7.0*	0.05	262145**	0.04	0.04
H/Prop 1970	3	59.8**	9.9**	0.02	293992**	0.03	0.05

Table 52. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for sink traits (Table 50) of maize hybrids grown at three plant densities in four environments

Source	df	Mean squares					
		Ear length	Kernel depth	Kernel weight	Kernel number/ plant	Total ears/ plant	MH ears/ plant
Hybrid x environment (E)	69	3.9**	2.2**	0.01	31562**	0.02**	0.05**
Decades x E	15	4.0	2.8**	0.02	44417**	0.04**	0.07**
Public decades x E	12	4.5	3.2**	0.01	50835**	0.04**	0.09**
Linear x E	3	2.6	3.2*	0.01	70416**	0.09**	0.24**
Quadratic x E	3	5.9	5.6**	0.02	39115*	0.03*	0.05**
Cubic x E	3	7.7*	3.0*	0.01	84430**	0.04**	0.05**
Lack of fit x E	3	1.6	1.0	0.00	9380	0.01	0.01
1970 vs Prop 1970 x E	3	2.3	1.1	0.03	18745	0.01	0.02
Hybrids/decades x E	54	3.9*	2.1**	0.01	27991**	0.02*	0.04**
H/1930 x E	9	3.3	6.8**	0.00	19696	0.02*	0.13**
H/1940 x E	9	4.7	1.1	0.00	14732	0.01	0.04**
H/1950 x E	9	5.1*	0.9	0.00	15557	0.02*	0.01
H/1960 x E	9	1.4	1.1	0.00	56655**	0.03**	0.03**
H/1970 x E	9	4.2	1.7	0.05**	38887**	0.04**	0.03**
H/Prop 1970 x E	9	4.8	0.8	0.00	22419*	0.01	0.01

Table 53. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for ear-sink traits (Table 50) of maize hybrids grown at three plant densities in four environments

Source	*df*	Mean squares					
		Ear length	Kernel depth	Kernel weight	Kernel number/ plant	Total ears/ plant	MH ears/ plant
Hybrid x density (D)	46	3.1	3.2**	0.01	18622*	0.02**	0.02**
Decades x D	10	2.0	2.9	0.01	21694*	0.03**	0.04**
Public decades x D	8	2.5	3.6*	0.01	24562	0.03**	0.04**
Linear x D	2	1.9	1.1	0.03**	67111**	0.10**	0.08**
Quadratic x D	2	0.7	4.6	0.01	6047	0.03*	0.02*
Cubic x D	2	3.7	5.5*	0.00	9257	0.00	0.06**
Lack of fit x D	2	3.6	3.0	0.00	15834	0.00	0.01
1970 vs Prop 1970 x D	2	0.1	0.2	0.02	10222	0.01	0.01
Hybrids/decades x D	36	3.5	3.3**	0.01	17768*	0.01	0.02**
H/1930 x D	6	2.5	12.2**	0.00	12239	0.02	0.04**
H/1940 x D	6	5.0	3.9*	0.00	46588**	0.02	0.03**
H/1950 x D	6	10.0**	1.1	0.00	17019	0.01	0.01
H/1960 x D	6	1.3	0.9	0.00	7188	0.02	0.01
H/1970 x D	6	1.2	0.4	0.07**	5076	0.01	0.01
H/Prop 1970 x D	6	0.7	1.5	0.00	18500	0.00	0.00

Table 54. Environment x decade means for kernel depth of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
	mm				
1930	8.0	8.6	9.7	9.6	1.7
1940	9.8	9.7	10.3	9.7	0.6
1950	9.4	9.0	9.9	9.5	0.9
1960	9.4	9.3	10.4	9.7	1.1
1970	9.7	9.6	10.5	10.1	1.0
Prop 1970	9.3	9.8	10.6	10.1	1.3
$\bar{X}$	9.3	9.3	10.2	9.8	0.9

$LSD_{0.05}$ = 0.5 mm across environments within a decade

Table 55. Environment x decade means for kernel number per plant of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
1930	390.5	458.2	507.1	708.4	317.9
1940	591.2	579.0	590.3	791.9	212.9
1950	483.8	582.0	569.6	669.0	185.2
1960	470.6	574.1	603.1	674.8	204.2
1970	581.3	634.8	600.1	767.7	186.4
Prop 1970	514.6	521.6	555.1	730.0	215.4
$\bar{X}$	505.3	558.4	571.2	723.2	217.9

$LSD_{0.05}$ = 50.2 kernels per plant across environments within a decade

Table 56. Environment x decade means for total ears per plant of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
1930	0.77	0.75	0.88	0.93	0.16
1940	0.92	0.85	0.97	0.97	0.05
1950	0.88	0.94	0.96	0.94	0.08
1960	0.87	0.96	0.99	0.97	0.12
1970	0.93	0.97	1.00	0.99	0.07
Prop 1970	0.91	0.91	1.00	0.97	0.09
$\bar{X}$	0.88	0.90	0.97	0.96	0.09

$LSD_{0.05}$ = 0.05 total ears per plant across environments within a decade

Table 57. Environment x decade means for machine-harvestable ears per plant of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1980	Ankeny 1981	Ames 1980	Range
1930	0.45	0.69	0.61	0.78	0.33
1940	0.72	0.83	0.74	0.90	0.18
1950	0.83	0.92	0.90	0.93	0.10
1960	0.86	0.95	0.97	0.96	0.11
1970	0.90	0.96	0.95	0.97	0.07
Prop 1970	0.90	0.90	0.98	0.95	0.07
$\bar{X}$	0.78	0.88	0.86	0.91	0.13

$LSD_{0.05}$ = 0.05 harvestable ears per plant across environments within a decade

Table 58. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for ear-sink traits for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrids	Density L	Density M	Density H	b_{lin}	b_{quad}
	Kernel number per plant				
1930	708.0	490.3	375.8	-166.1	17.2
1940	818.8	615.2	484.4	-157.2	12.1
1950	729.4	560.3	438.9	-145.3	8.0
1960	751.9	553.7	441.1	-155.4	14.3
1970	765.5	638.5	531.0	-117.3	3.2
Prop 1970	727.9	577.5	451.4	-138.3	4.1
$LSD_{0.05}$	44.7	44.7	44.7	31.6	18.2
	MH ears per plant				
1930	0.75	0.60	0.53	-0.11	0.01
1940	0.95	0.77	0.66	-0.15	0.01
1950	0.99	0.91	0.77	-0.11	-0.01
1960	1.01	0.93	0.86	-0.08	0.00
1970	1.04	0.93	0.86	-0.09	0.01
Prop 1970	1.01	0.95	0.86	-0.08	-0.01
$LSD_{0.05}$	0.04	0.04	0.04	0.03	0.02
	Total ears per plant				
1930	0.97	0.84	0.71	-0.13	0.00
1940	1.02	0.94	0.83	-0.10	-0.01
1950	1.00	0.95	0.84	-0.08	-0.01
1960	1.01	0.94	0.88	-0.07	0.00
1970	1.05	0.96	0.91	-0.07	0.01
Prop 1970	1.02	0.96	0.88	-0.07	0.00
$LSD_{0.05}$	0.04	0.04	0.04	0.03	0.02
	Kernel weight (g)				
1930	0.326	0.302	0.290	-0.018	0.0020
1940	0.306	0.292	0.279	-0.014	0.0002
1950	0.336	0.320	0.313	-0.012	0.0020
1960	0.337	0.323	0.316	-0.011	0.0010
1970	0.348	0.330	0.381	0.017	0.0120
Prop 1970	0.332	0.324	0.315	-0.009	-0.0002
$LSD_{0.05}$	0.042	0.042	0.042	0.030	0.0200

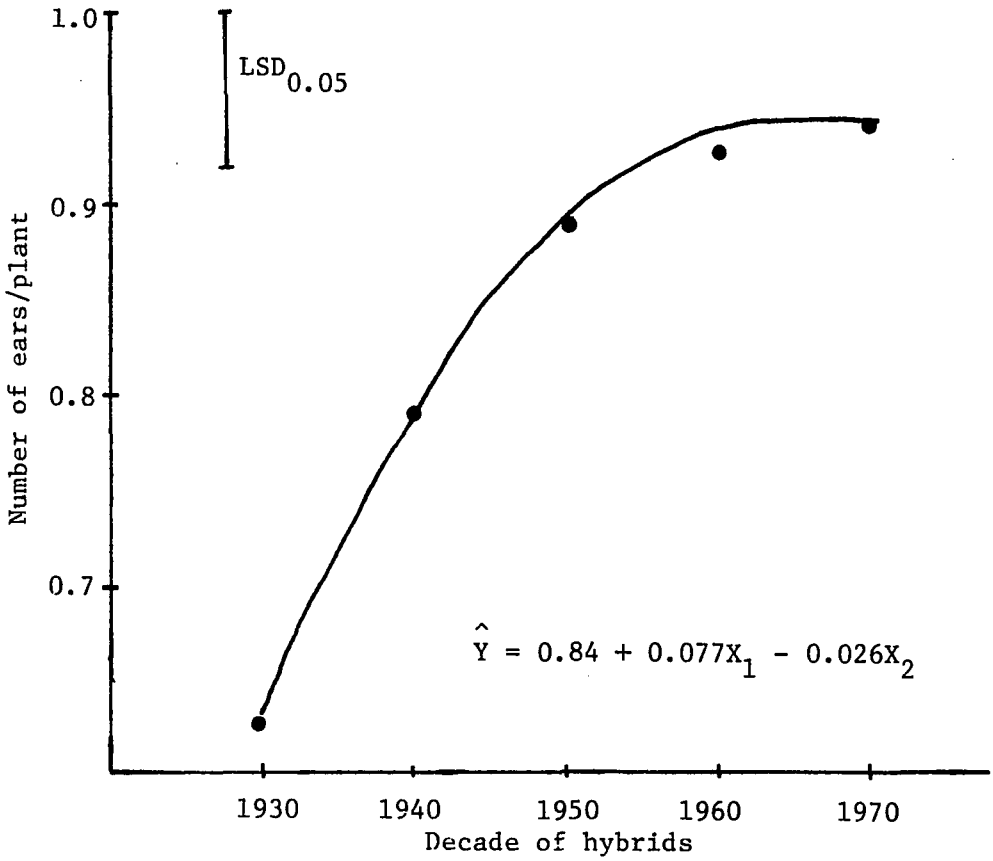

Figure 18. Predicted numbers of machine-harvestable ears per plant for hybrids based on actual numbers of machine-harvestable ears per plant of four public hybrids selected to represent each decade from 1930 to 1970

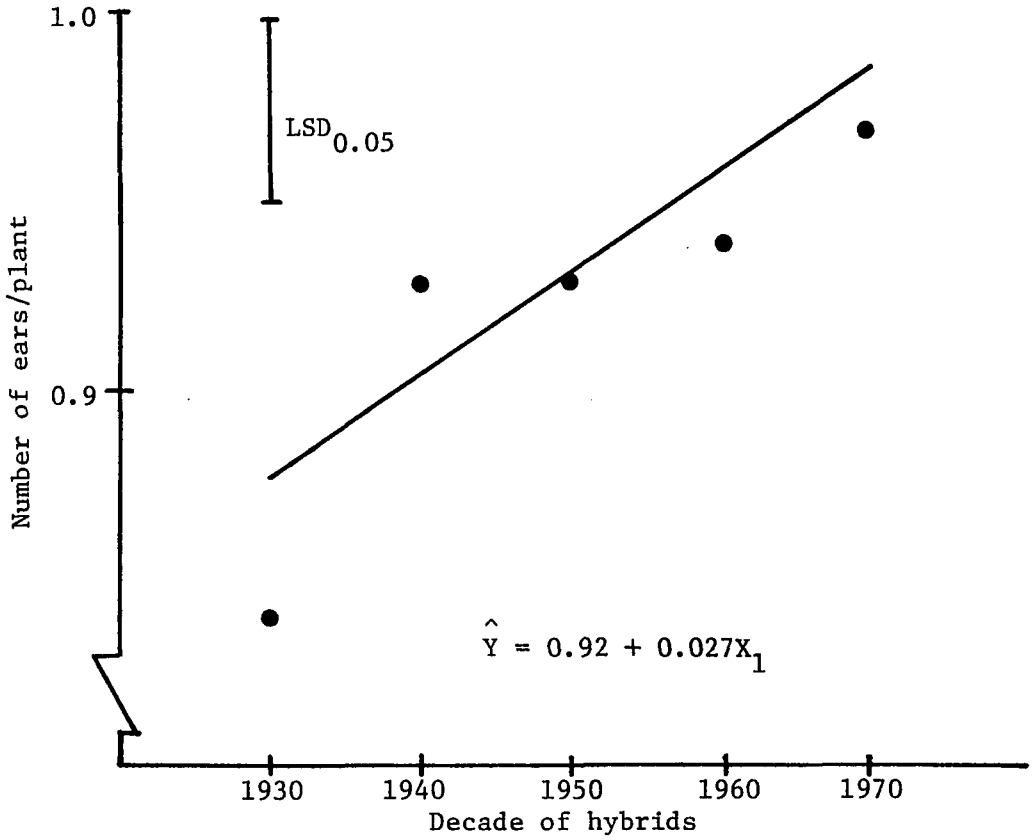

Figure 19. Predicted total numbers of ears per plant for hybrids at 10-year intervals based on actual total numbers of ears per plant of four public hybrids selected to represent each decade from 1930 to 1970

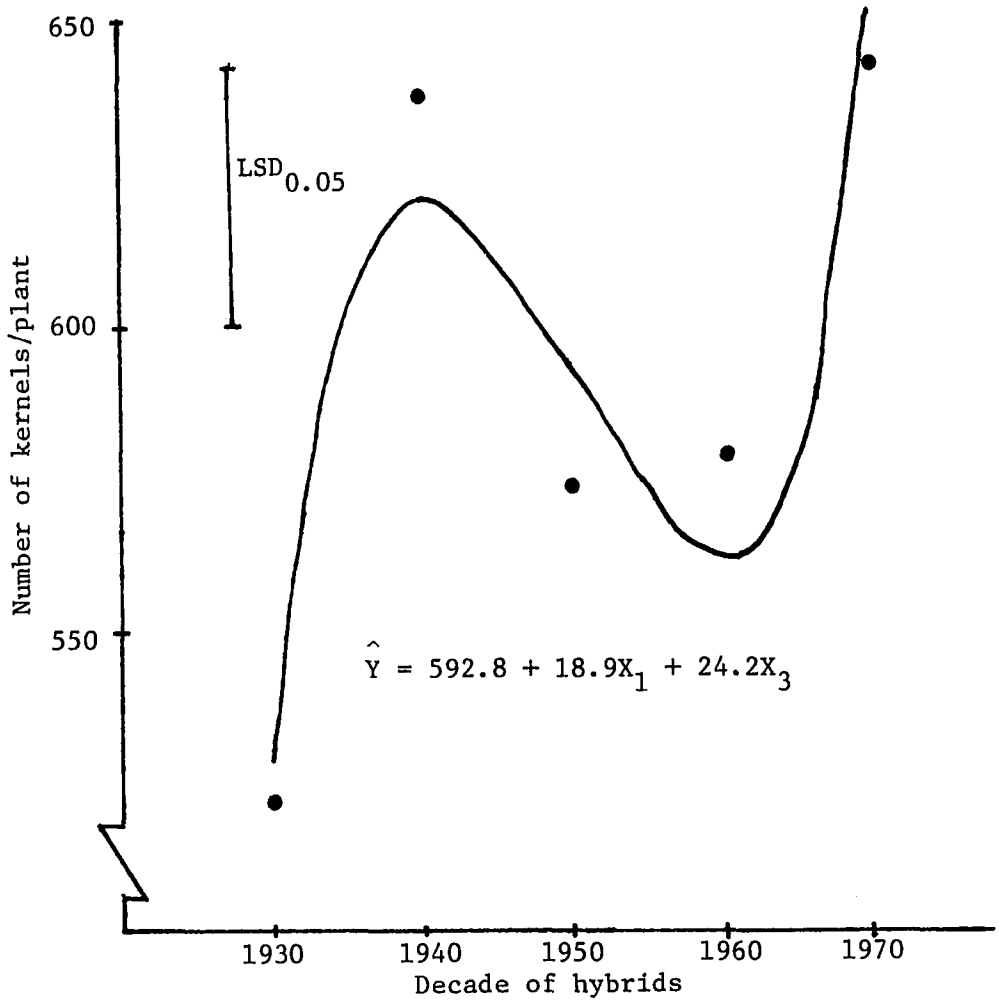

Figure 20. Predicted numbers of kernels per plant for hybrids at 10-year intervals based on actual numbers of kernels per plant of four public hybrids selected to represent each decade from 1930 to 1970

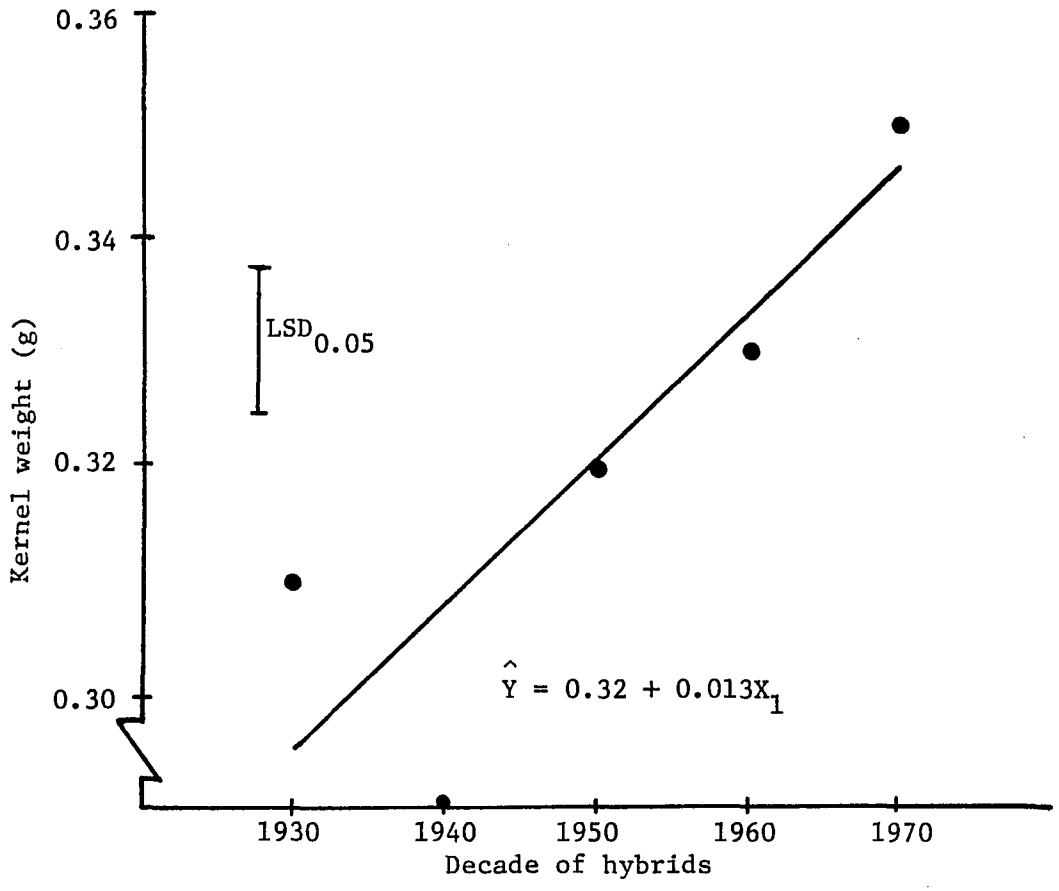

Figure 21. Predicted kernel weights for hybrids based on actual kernel weights of four public hybrids selected to represent each decade from 1930 to 1970

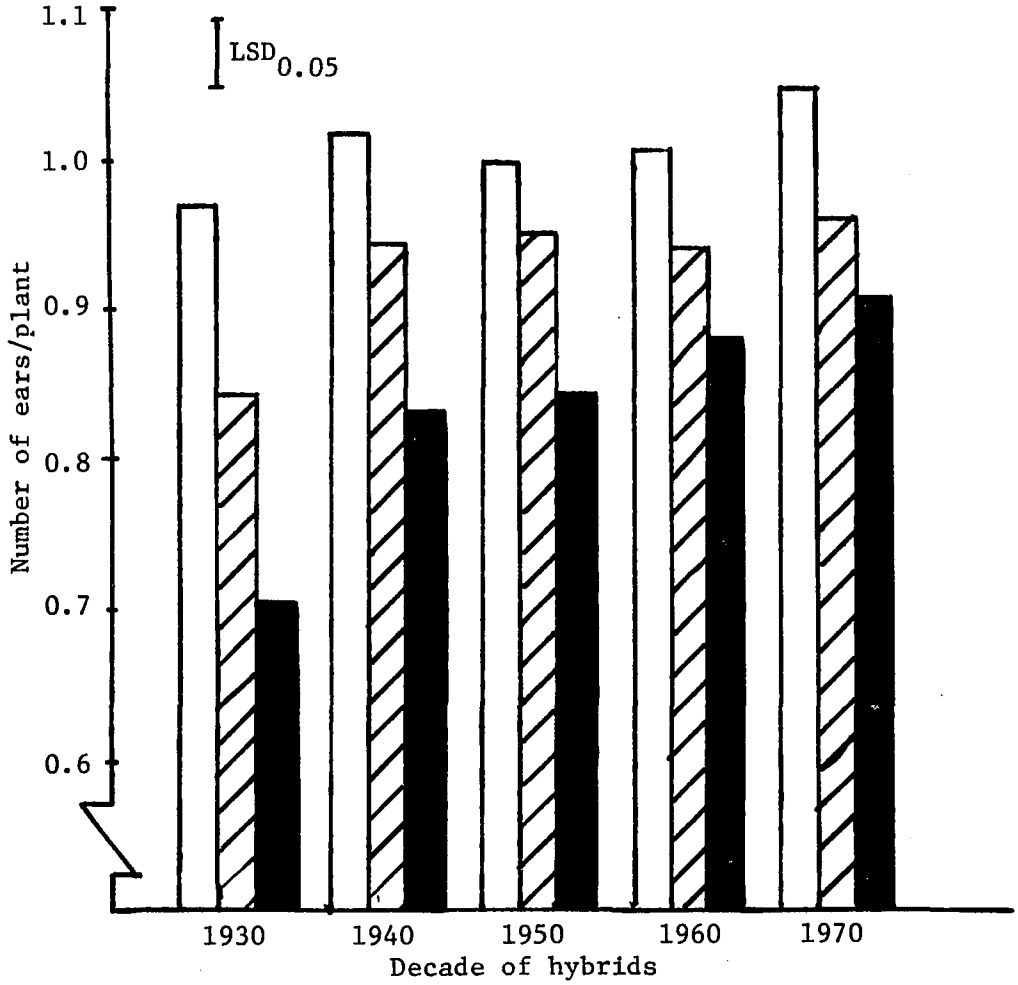

Figure 22. Mean total number of ears per plant at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

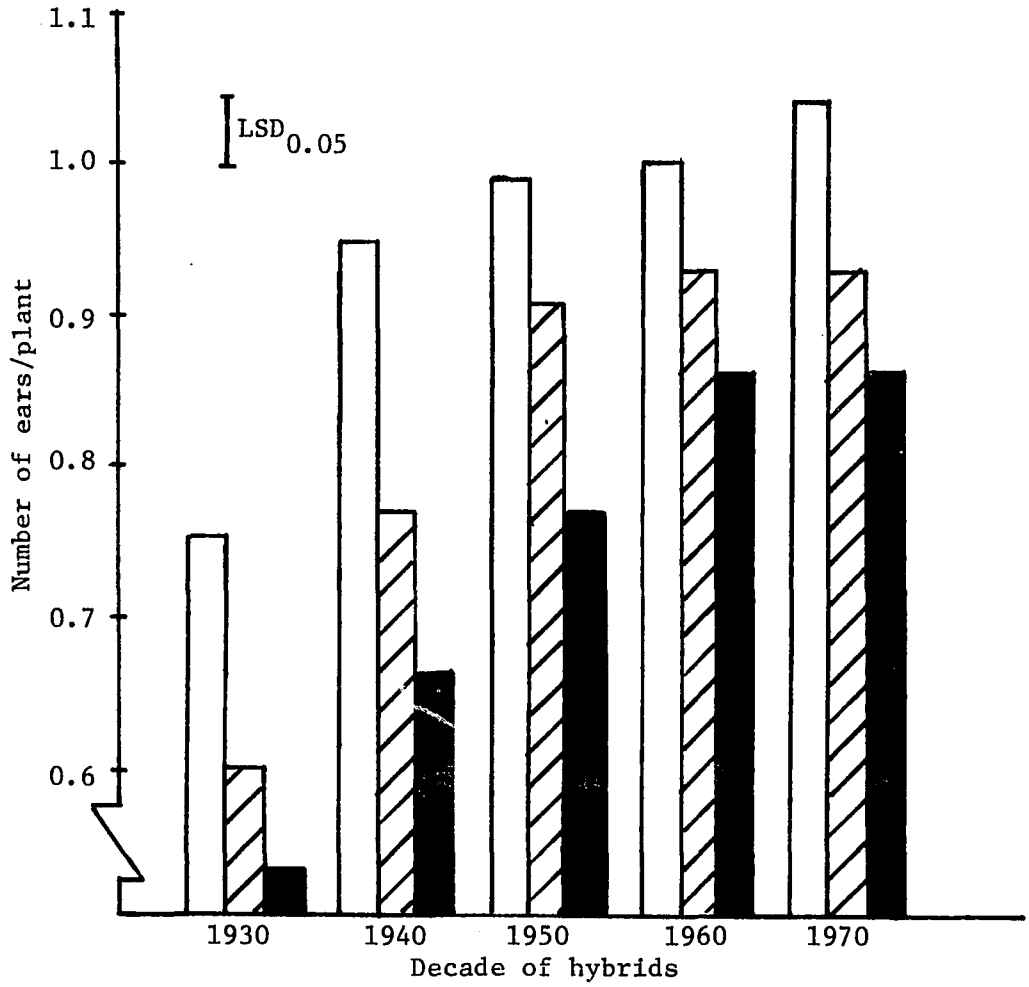

Figure 23. Mean machine-harvestable ears per plant at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

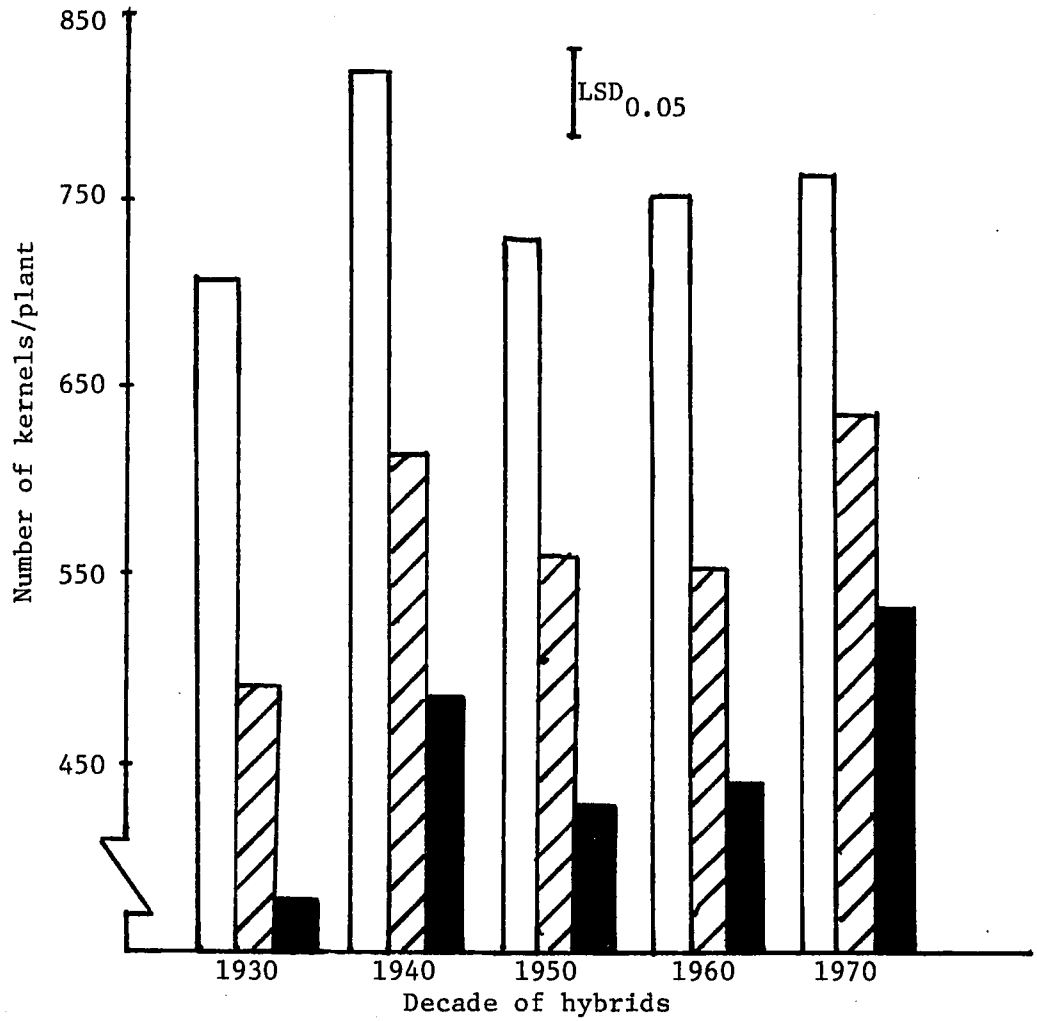

Figure 24. Mean number of kernels per plant at low (□), medium (▨), and high (■) plant densities of four public hybrids selected to represent each decade from 1930 to 1970

note the similarity between the cubic pattern of change across decades for kernel number per plant and total grain yield (Figures 20 and 2). For both traits, significant gains were made only between the 1930 and 1940 decades and the 1960 and 1970 decades (Tables 7 and 49). Although the increase in kernel depth between the 1930 and 1970 decades was only 1.0 mm, it represented an 11% increase (Table 49). The pattern of change across decades for kernel weight was linear (Figure 21). The range in kernel weights among decades, however, appears to be very small at 0.062 g per kernel (Table 49), but when multiplied by 591.0, the overall mean number of kernels per plant (Table 48), it represents a difference of 36.6 g of grain per plant.

The interaction of public decades with environments was significant for kernel depth, kernel number, total and machine-harvestable ears per plant (Table 52). Ear-sink size in the four most recent decades, as determined by these four traits, was not affected as adversely in the stress environment (Ames 1981) as it was for the 1930 hybrids (Tables 54, 55, 56, and 57). The greatest difference in stress tolerance occurred between the 1930 and 1940 decades for all four traits.

Mean squares for the public decades x density interaction were significant for kernel depth, total and machine-harvestable ears per plant (Table 53). Kernel weight and kernel number exhibited significant linear x density inter-

actions (Table 53). The linear regression coefficient for kernel weight across plant densities was 0.017 g for the 1970 decade unlike the negative responses found in all preceding decades (Table 58). Figures 22 and 23 illustrate the number of total and machine-harvestable ears per plant for each decade at each plant density. Although total number of ears per plant at the low plant density was similar for all decades, the number of machine-harvestable ears per plant at this density increased from 0.75 in the 1930 decade to 1.04 in the 1970 decade (Table 58). At high plant densities, however, the 1930 hybrids produced significantly less total and machine-harvestable ears per plant than did the 1970 hybrids (Table 58). Figure 24 illustrates that significant increases in kernel number per plant at high plant density occurred between the 1930 and 1940 decades and the 1960 and 1970 decades. Linear regression coefficients for total ears per plant, machine-harvestable ears per plant, and kernel number per plant across plant densities significantly increased over decades (Table 58). This indicates that 1970 hybrids were more capable of maintaining their ear-sink size at high plant densities than their earlier counterparts; hence, the 1970 group was more density tolerant.

Flowering Traits

Data for flowering traits are given in Tables 59-64 and illustrated by Figure 25. Flowering, evaluated both in days from July 1 and accumulated heat units from planting, was significantly earlier at Ankeny in both 1980 and 1981 than at Ames in either 1980 or 1981 (Table 59). The ranges for 50% pollen shed and 50% silking dates across environments were 6.8 and 8.9 days, respectively (Table 59). Environment had a significant effect on both the silking and pollen-shed intervals with ranges across environments of 2.9 days and 1.0 day, respectively (Table 59). The longest pollen-shed-to-silking interval was 4.3 days at Ames in 1981 and the shortest was 1.3 days at Ankeny in 1981 (Table 59).

Mean squares for plant densities were significant for all flowering traits except the pollen-shed and silking intervals (Table 61). Increasing plant densities delayed flowering. The pollen-shed-to-silking interval increased 2.1 days as plant density was increased (Table 59).

Public decades displayed significantly different pollen-shed and silking dates (Table 62). The 1930 decade had the earliest 50% pollen-shed and 50% silking dates and the 1950 decade had the latest (Table 60). The ranges over decades for 50% pollen shed and 50% silking, however, were only 3.2 and 2.8 days, respectively. With a range of only 49.7 heat units from planting to silking among all decades, the desired

Table 59. Means for flowering traits of 24 single-cross hybrids grown at three plant densities in four environments

	Pollen shed			Silk extrusion			Interval			Heat units to 50% silk
	25%	50%	75%	25%	50%	75%	Silking	Pollen shed	Pollen-shed-to silk	
	(days after July 1)						(days)			
Ames 1980	16.0	17.3	19.1	18.2	20.0	22.2	4.0	3.1	2.7	911.2
Ames 1981	18.2	19.4	20.9	21.9	23.7	25.7	3.8	2.6	4.3	909.1
Ankeny 1980	11.2	12.6	14.6	13.3	15.1	19.0	5.7	3.4	2.7	842.2
Ankeny 1981	12.4	13.4	14.7	13.6	14.8	16.4	2.8	2.4	1.3	860.6
$LSD_{0.05}$	0.5	0.6	0.8	0.7	0.8	2.1	2.0	0.4	1.0	7.0
Density L	14.0	15.2	16.7	15.6	16.9	18.6	3.1	2.6	1.7	859.9
Density M	14.4	15.6	17.2	16.6	18.4	20.7	4.1	2.8	2.8	880.6
Density H	15.0	16.4	18.3	18.1	20.0	23.3	5.2	3.3	3.8	901.8
$LSD_{0.05}$	0.5	0.5	0.7	0.6	0.7	1.8	1.8	0.4	0.9	6.1
Overall $\bar{X}$	14.5	15.7	17.4	16.8	18.4	20.9	4.1	2.9	2.8	880.8
C.V. %	10.7	10.8	11.6	10.5	10.4	11.7	41.4	44.5	54.4	1.9

Table 60. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for flowering traits of four public single-cross maize hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in four environments

	Pollen shed			Silk extrusion			Interval			
	25%	50%	75%	25%	50%	75%	Silking	Pollen shed	Pollen-shed-to silk	Heat units to 50% silk
	(days after July 1)						(days)			
1930	12.9	13.9	15.5	15.1	17.0	19.7	4.6	2.7	3.1	861.0
1940	14.1	15.6	17.3	17.1	18.6	21.3	4.2	3.0	3.1	884.7
1950	15.9	17.1	18.9	18.6	20.4	22.5	3.9	2.9	3.3	907.8
1960	14.8	16.1	17.7	17.3	19.0	21.5	4.3	2.9	3.0	887.8
1970	15.2	16.5	18.1	17.2	18.8	21.1	3.9	2.9	2.4	885.3
Prop 1970	13.9	15.1	16.9	15.2	16.8	19.2	3.9	2.9	1.8	858.1
$LSD_{0.05}$	0.5	0.6	0.7	0.4	0.5	0.8	0.6	0.3	0.6	7.1
b_1	0.54± 0.05	0.58± 0.06	0.57± 0.06	0.43± 0.05	0.38± 0.05	0.30± 0.09	-0.13± 0.06	0.04± 0.03	-0.17± 0.06	5.2± 0.8
b_q	-0.33± 0.01	-0.36± 0.02	-0.39± 0.02	-0.51± 0.01	-0.48± 0.01	-0.45± 0.02	0.04± 0.02	-0.04± 0.01	-0.12± 0.02	-6.8± 0.7
b_c	0.12 ± 0.05	0.16± 0.06	0.17± 0.06	0.15± 0.05	0.10± 0.05	0.09± 0.09	-0.08± 0.06	0.06± 0.03	-0.06± 0.06	1.8± 0.8

Table 61. Mean squares from combined analyses of variance for flowering traits of 24 maize hybrids grown at three plant densities in four environments

		Mean squares			
		Pollen shed			
Source	df	25%	50%	75%	25%
Environment (E)	3	2224.8	2197.0	2105.3	3609.6
Reps/E	8	13.2	14.7	25.8	16.1
Density (D)	2	75.0*	99.8*	194.5**	470.3**
D x E	6	10.3	11.5	24.0	19.2
Error a	16	6.1	8.1	12.9	10.1
Hybrid (H)	23	59.8**	68.5**	75.7**	71.6**
H x E	69	4.2**	5.6**	4.6	3.7
H x D	46	2.2	2.7	2.7	1.9
H x D x E	138	2.2	2.7	3.9	2.4
Error b[a]	552	2.4	2.9	4.1	3.1

[a]Degrees of freedom for error b: 25% pollen shed, 544; 50% pollen shed, 540; 75% pollen shed, 538; 25% silk extrusion, 548; 50% silk extrusion, 546; 75% silk extrusion, 544; silking interval, 543; pollen shed interval, 543; pollen-shed-to-silk interval, 536; heat units to 50% silk, 552.

Mean squares					
		Interval			
Silk extrusion					
50%	75%	Silking	Pollen shed	Pollen-shed-to silk	Heat units to 50% silk
3840.8	3464.8	304.6	46.9	312.0	260885.4
18.1	31.0	10.5	7.8	18.9	2464.0
712.3**	1565.2**	324.2	30.1	301.0**	126211.3**
26.6	80.2*	74.1**	8.0	17.7*	3782.1
10.7	15.5	3.8	3.4	4.7	1565.3
69.0**	63.5**	7.8	2.8*	24.1**	13297.1**
3.9	11.2**	5.9**	1.3	5.7**	1087.3
2.3	4.0	3.2	1.6	2.9	563.7
3.6	5.9	3.4	1.5	2.8	837.6
3.7	6.0	2.9	1.7	2.3	906.2

Table 62. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for flowering traits (Table 61)

		Mean squares		
		Pollen shed		
Source	df	25%	50%	75%
Hybrid	23	59.8**	68.5**	75.7**
Decades	5	178.8**	205.5**	207.7**
Public decades	4	191.1**	219.3**	226.5**
Linear	1	414.4**	490.7**	460.4**
Quadratic	1	222.5**	263.9**	304.2**
Cubic	1	19.8*	35.0	43.6*
Lack of fit	1	107.6**	87.5*	97.9**
1970 vs Prop 1970	18	130.0**	150.7**	132.1**
Hybrids/decades	18	26.7**	30.4**	39.0**
H/1930	3	7.5	17.2*	29.5**
H/1940	3	70.7**	78.5**	68.8**
H/1950	3	21.5**	22.8*	26.9**
H/1960	3	19.8**	20.7*	28.3**
H/1970	3	33.4**	33.7**	62.0**
H/Prop 1970	3	7.6	9.6	18.4**

Mean squares						
Silk extrusion			Interval			
25%	50%	75%	Silking	Pollen shed	Pollen-shed-to silk	Heat units to 50% silk
71.6**	69.0**	63.5**	7.8	2.8	24.1**	13297.1**
234.0**	218.9**	171.6**	9.5	2.3	20.7**	42467.0**
225.6**	201.8**	148.8**	11.8	2.8	19.5*	39767.4**
269.3**	212.4**	131.4**	26.1	2.2	39.2*	38595.6**
520.6**	460.8**	410.0**	3.4	3.6	30.6*	94032.0**
33.1**	15.0	10.9	9.7	4.8	4.3	4640.4*
79.7**	118.8**	42.9	8.1	0.5	4.0	21801.6**
267.5**	287.6**	262.8**	0.2	0.2	25.2*	52365.6**
26.5**	27.3**	33.5**	7.3	2.9*	25.0**	5194.4**
4.5	3.5	2.5	4.3	8.1**	10.4	615.6
8.2	5.4	18.7	25.7**	1.0	75.8**	936.0
10.8*	8.3	16.8	2.3	1.6	11.2	1255.2
36.0*	55.4*	77.0**	7.4	1.6	9.7	11005.2**
58.8**	49.0**	46.6**	2.6**	2.4	16.7*	10047.6**
40.8**	42.2**	39.4*	1.5	2.8	26.3	7306.8**

Table 63. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for flowering traits (Table 61) of maize hybrids grown at three plant densities in four environments

		Mean squares		
		Pollen shed		
Source	df	25%	50%	75%
Hybrid x environment (E)	69	4.2**	5.6**	4.6
Decades x E	15	5.9**	10.4**	8.9**
Public decades x E	12	6.2**	11.9**	9.1**
Linear x E	3	9.4**	15.7**	13.3*
Quadratic x E	3	5.5	8.0*	5.0
Cubic x E	3	1.7	1.7	5.9
Lack of fit x E	3	8.3*	10.3*	12.4*
1970 vs Prop 1970 x E	3	4.4	4.4	8.1
Hybrids/decades x E	54	3.7*	4.3*	3.3
H/1930 x E	9	2.1	2.2	5.9
H/1940 x E	9	3.2	3.8	4.9
H/1950 x E	9	3.9	4.7	4.7
H/1960 x E	9	4.1	4.2	5.4
H/1970 x E	9	3.2	3.6	2.1
H/Prop 1970 x E	9	5.8*	7.2**	7.1

Mean squares						
Silk extrusion			Interval			Heat units to 50% silk
25%	50%	75%	Silking	Pollen shed	Pollen-shed-to silk	
3.7	3.9	11.2**	5.9**	1.3	5.7**	1087.3
4.8*	1.4	3.5	4.7	2.2	5.9**	1560.7
5.6*	3.5	4.1	5.7*	2.2	5.9**	1620.4
4.1	2.4	7.2	10.0*	1.2	9.2**	1382.1
3.9	2.9	0.9	1.5	1.2	4.9	1969.8
11.3*	6.7	2.3	5.7	3.6	4.1	1871.7
3.1	1.8	6.2	5.7	2.9	5.6	1257.9
0.6	0.6	1.1	0.8	2.0	5.7	1321.8
3.4	4.7	10.9**	6.2**	1.1	5.7**	955.8
1.3	2.0	14.1*	13.7**	2.0	3.8	328.7
1.9	1.4	5.2	7.7**	1.2	3.2	218.5
3.4	5.1	7.1	2.0	1.2	1.1	1121.9
8.6**	10.3**	20.3**	8.8**	0.9	10.6**	2350.0**
2.4	4.7	3.9	0.9	0.5	2.9	981.1
2.8	4.5	6.6	4.0	0.7	12.4**	734.5

Table 64. Mean squares derived from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for flowering traits (Table 61) for maize hybrids grown at three plant densities in four environments

		Mean squares		
		Pollen shed		
Source	df	25%	50%	75%
Hybrid x density (D)	46	2.2	2.7	2.7
Decades x D	10	1.6	2.6	2.2
Public decades x D	8	1.6	2.8	2.6
Linear x D	2	2.7	4.9	2.4
Quadratic x D	2	1.2	0.3	1.4
Cubic x D	2	1.2	5.5	5.8
Lack of fit x D	2	1.5	0.6	0.8
1970 vs Prop 1970 x D	2	1.4	1.4	0.5
Hybrids/decades x D	36	2.2	2.8	2.8
H/1930 x D	6	1.2	0.8	2.7
H/1940 x D	6	1.1	2.2	3.8
H/1950 x D	6	1.1	0.7	3.1
H/1960 x D	6	1.7	2.2	1.1
H/1970 x D	6	2.7	3.9	2.2
H/Prop 1970 x D	6	6.0*	6.8*	3.9

Mean squares						
Silk extrusion			Interval			Heat units to 50% silk
25%	50%	75%	Silking	Pollen shed	Pollen-shed-to-silk	
1.9	2.3	4.0	3.2	1.6	2.9	563.7
2.5	1.4	4.1	4.2	1.7	2.2	350.0
1.7	1.1	4.3	4.4	1.9	2.2	161.1
1.7	0.3	5.2	8.2	1.9	2.3	73.8
1.0	1.3	7.5	3.6	0.8	0.4	142.2
1.8	2.6	3.9	3.1	2.4	5.3	418.8
2.6	0.4	0.8	2.7	2.5	0.7	9.6
5.3	2.5	3.1	3.1	1.0	2.3	1105.8
1.8	2.6	4.0	2.9	1.6	3.0	623.0
0.8	1.5	5.3	5.1	3.4	2.1	402.8
1.5	3.0	5.1	2.4	2.0	4.3	952.2
2.4	4.0	4.4	2.0	0.9	1.7	1205.2
2.5	1.1	1.2	2.3	0.8	0.8	299.2
1.6	3.3	5.9	3.9	1.2	1.2	385.4
1.8	2.8	2.0	1.6	1.1	8.1**	493.2

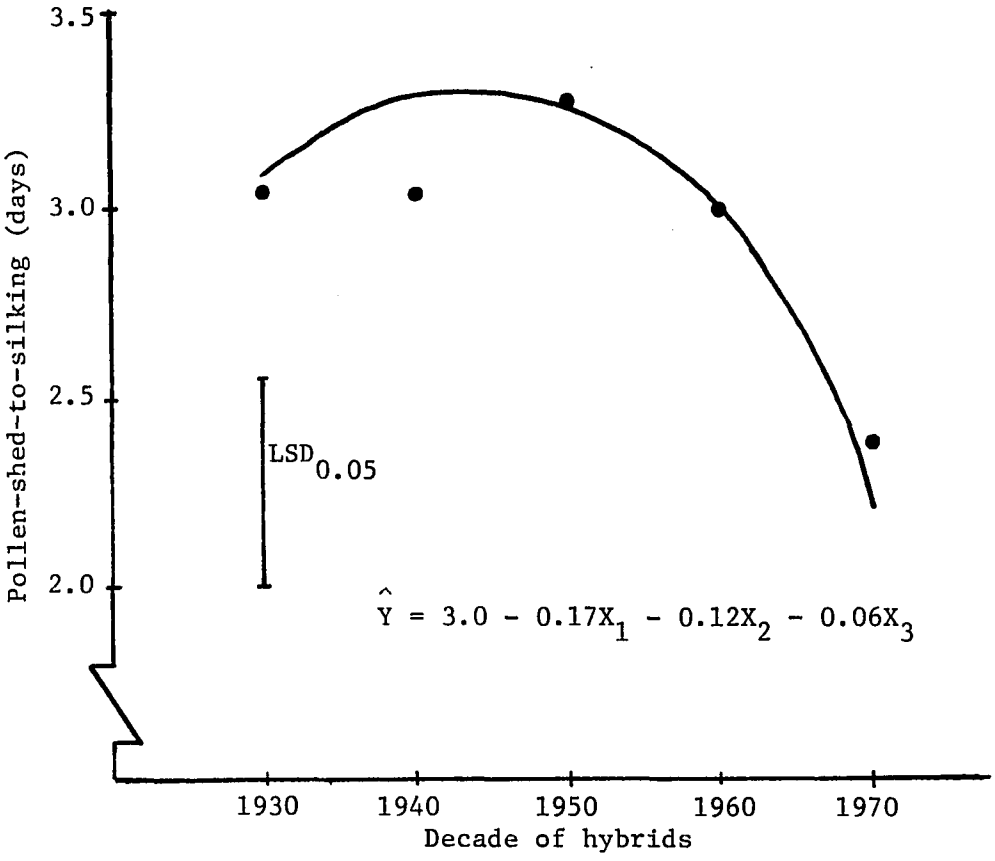

Figure 25. Predicted pollen-shed-to-silking intervals for hybrids based on actual pollen-shed-to-silking intervals of four public hybrids selected to represent each decade from 1930 to 1970

similarity of maturity among decades appears to have been achieved (Table 60). Although differences among decades for pollen-shed and silking intervals were not significant, the pollen-shed-to-silking interval did vary significantly across decades (Table 60). A linear decrease of 0.17 ± 0.06 days in the pollen-shed-to-silking interval per decade was found to be significant (Tables 60 and 62 and Figure 25). The decrease in the pollen-shed-to-silking interval between the 1930 and 1970 decades was 0.7 days (Table 60). The 1970 proprietary hybrids displayed the shortest pollen-shed-to-silking interval, i.e., 1.8 days.

Mean squares for public decades x environment interactions were significant for all pollen-shed traits, 25% silk extrusion, the silking interval, and the pollen-shed-to-silking interval (Table 63). Decade by environment means for these traits were examined and it was noted that all decades flowered latest and had the longest pollen-shed-to-silking interval in the lowest yielding environment, i.e., Ames 1981. No other interpretations of these interactions could be made.

The relative responses of the public decades to plant densities were not significantly different (Table 64).

Heat Unit Efficiency Traits

Data for heat unit efficiency traits are given in Tables 65-73. The effect of environment on dry matter accumulation

Table 65. Means for heat unit efficiency traits of 24 single-cross maize hybrids grown at three plant densities in three environments[a]

	VEG1	VEG2	VEG3	GF	VFGGF
	g/heat unit				
Ames 1980	0.0166	0.3409	0.1916	0.1833	-0.0200
Ames 1981	0.0035	0.2409	0.1695	0.2667	0.0427
Ankeny 1981	0.0089	0.3067	0.1881	0.2953	0.0370
$LSD_{0.05}$	0.0010	0.0180	0.0093	0.0423	0.0256
Density L	0.0099	0.3614	0.2207	0.3167	0.0392
Density M	0.0096	0.2874	0.1775	0.2369	0.0157
Density H	0.0094	0.2394	0.1509	0.1922	0.0052
$LSD_{0.05}$	0.0010	0.0180	0.0093	0.0423	0.0256
Overall $\bar{X}$	0.0096	0.2961	0.1831	0.2485	0.0120
C.V. %	28.6	15.0	13.9	20.8	234.8

[a]Hereinafter, VEG1 is the rate of dry matter accumulation per heat unit from planting to a juvenile stage; VEG2 is the rate of dry matter accumulation per heat unit from a juvenile stage to 50% silk; VEG3 is the rate of dry matter accumulation per heat unit from planting to 50% silk; GF is the rate of dry matter accumulation per heat unit from 50% silk to harvest; and VEGGF is the rate of vegetative dry matter accumulation per heat unit from 50% silk to harvest.

Table 66. Means and linear (b_1), quadratic (b_q), and cubic (b_c) regression coefficients for heat unit efficiency traits of four public single-cross maize hybrids selected to represent each decade from 1930 to 1970 and four proprietary hybrids from the 1970 decade grown at three plant densities in three environments

Decade of hybrids	VEG1	VEG2	VEG3	GF	VEGGF
	g/heat unit				
1930	0.0091	0.2788	0.1707	0.1904	-0.0127
1940	0.0093	0.2870	0.1779	0.2189	-0.0069
1950	0.0092	0.2904	0.1824	0.2598	0.0233
1960	0.0101	0.3084	0.1917	0.2803	0.0537
1970	0.0107	0.3229	0.1998	0.2809	0.0275
Prop 1970	0.0095	0.2894	0.1761	0.2609	0.0350
$LSD_{0.05}$	0.0010	0.0157	0.0090	0.0169	0.0190
b_1	0.0004± 0.0001	0.0110± 0.0017	0.0072± 0.0010	0.0242± 0.0021	0.0046± 0.0019
b_q	0.0001± 0.0001	0.0019± 0.0015	0.0005± 0.0009	-0.0055± 0.0018	-0.0082± 0.0016
b_c	-0.0000± 0.0001	0.0001± 0.0017	0.0001± 0.0010	-0.0033± 0.0021	-0.0040± 0.0019

Table 67. Mean squares from combined analyses of variance for heat unit efficiency traits of maize hybrids grown at three plant densities in three environments

Source	df	Mean squares				
		VEG1	VEG2	VEG3	GF	VEGGF
Environment (E)	2	0.0093899	0.5574	0.0305	0.7257	0.2579
Reps/E	6	0.0000705	0.0037	0.0015	0.0037	0.0036
Density (D)	2	0.0000257	0.8148**	0.2676**	0.8525**	0.0649*
D x E	4	0.0000371	0.0064	0.0008	0.0248*	0.0092*
Error a	12	0.0003742	0.0083	0.0025	0.0043	0.0026
Hybrid (H)	23	0.0000392**	0.0119**	0.0051**	0.0428**	0.0173**
H x E	46	0.0000133**	0.0033**	0.0011**	0.0048**	0.0038**
H x D	46	0.0000059	0.0028	0.0010	0.0042*	0.0034*
H x D x E	92	0.0000054	0.0023	0.0008*	0.0029	0.0020
Error b[a]	414	0.0000075	0.0020	0.0006	0.0027	0.0022

[a]Degrees of freedom for error b: VEG1, 414; VEG2, 413; VEG3, 413; GF, 410; VEGGF, 410.

Table 68. Mean squares derived from partitioning of hybrid sums of squares from combined analyses of variance for heat unit efficiency traits (Table 67)

Source	df	Mean squares				
		VEG1	VEG2	VEG3	GF	VEGGF
Hybrid	23	0.0000392**	0.0119**	0.0051**	0.0428**	0.0173**
Decades	5	0.0000583**	0.0397**	0.0174**	0.1433**	0.0650**
Public decades	4	0.0000533**	0.0344**	0.0142**	0.1737**	0.0805**
Linear	1	0.0001755**	0.1298**	0.0560**	0.6352**	0.2160**
Quadratic	1	0.0000297	0.0057	0.0003	0.0462**	0.0326**
Cubic	1	0.0000000	0.0000	0.0000	0.0719**	0.0114
Lack of fit	1	0.0000081	0.0023	0.0003	0.0020	0.0015
1970 vs Prop 1970	1	0.0000783*	0.0606**	0.0302**	0.0217*	0.0030
Hybrids/decades	18	0.0000339**	0.0042	0.0017	0.0149**	0.0041
H/1930	3	0.0000504*	0.0094*	0.0039*	0.0542**	0.0091
H/1940	3	0.0000207	0.0103*	0.0038*	0.0008	0.0015
H/1950	3	0.0000036	0.0014	0.0007	0.0057	0.0121
H/1960	3	0.0000783**	0.0022	0.0012	0.0028	0.0018
H/1970	3	0.0000054	0.0011	0.0004	0.0128	0.0040
H/Prop 1970	3	0.0000450*	0.0011	0.0004	0.0065	0.0026

Table 69. Mean squares derived from partitioning of hybrid x environment interaction sums of squares from combined analyses of variance for heat unit efficiency traits (Table 67) of maize hybrids grown at three plant densities in three environments

Source	df	Mean squares				
		VEG1	VEG2	VEG3	GF	VEGGF
Hybrid x environment (E)	46	0.0000133**	0.0033**	0.0011**	0.0048**	0.0038**
Decades x E	10	0.0000201**	0.0050**	0.0013*	0.0090**	0.0068**
Public decades x E	8	0.0000184**	0.0060**	0.0015*	0.0106**	0.0076**
Linear x E	2	0.0000392**	0.0150**	0.0036**	0.0297**	0.0220**
Quadratic x E	2	0.0000132	0.0050	0.0016	0.0090*	0.0005
Cubic x E	2	0.0000009	0.0027	0.0005	0.0018	0.0031
Lack of fit x E	2	0.0000207	0.0013	0.0005	0.0020	0.0050
1970 vs Prop 1970 x E	2	0.0000266*	0.0011	0.0003	0.0025	0.0036
Hybrids/decades x E	36	0.0000114*	0.0028	0.0010*	0.0037	0.0030
H/1930 x E	6	0.0000096	0.0040	0.0015*	0.0065*	0.0039
H/1940 x E	6	0.0000036	0.0036	0.0013*	0.0005	0.0023
H/1950 x E	6	0.0000172*	0.0013	0.0006	0.0044	0.0014
H/1960 x E	6	0.0000250**	0.0047*	0.0019**	0.0039	0.0042
H/1970 x E	6	0.0000046	0.0015	0.0005	0.0022	0.0013
H/Prop 1970 x E	6	0.0000087	0.0017	0.0005	0.0046	0.0050

Table 70. Mean squares from partitioning of hybrid x density interaction sums of squares from combined analyses of variance for heat unit efficiency traits (Table 67) of maize hybrids grown at three plant densities in three environments

Source	df	Mean squares				
		VEG1	VEG2	VEG3	GF	VEGGF
Hybrid x density (D)	46	0.0000059	0.0028	0.0010	0.0042*	0.0034*
Decades x D	10	0.0000048	0.0040*	0.0012	0.0046	0.0055**
Public decades x D	8	0.0000039	0.0031	0.0008	0.0050	0.0064**
Linear x D	2	0.0000004	0.0017	0.0004	0.0061	0.0116**
Quadratic x D	2	0.0000058	0.0008	0.0002	0.0080	0.0023
Cubic x D	2	0.0000085	0.0067*	0.0018	0.0045	0.0090*
Lack of fit x D	2	0.0000009	0.0032	0.0010	0.0014	0.0026
1970 vs Prop 1970 x D	2	0.0000081	0.0075*	0.0027*	0.0029	0.0021
Hybrids/decades x D	36	0.0000063	0.0025	0.0009	0.0040*	0.0028
H/1930 x D	6	0.0000052	0.0040	0.0014	0.0119**	0.0060*
H/1940 x D	6	0.0000067	0.0034	0.0015	0.0040	0.0037
H/1950 x D	6	0.0000034	0.0011	0.0005	0.0029	0.0017
H/1960 x D	6	0.0000075	0.0015	0.0005	0.0007	0.0010
H/1970 x D	6	0.0000075	0.0011	0.0004	0.0025	0.0026
H/Prop 1970 x D	6	0.0000073	0.0036	0.0011	0.0022	0.0024

Table 71. Environment x decade means for rate of dry matter accumulation per heat unit between planting and a juvenile stage (VEG1) group of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1981	Ames 1980	Range
	g/heat unit			
1930	0.0035	0.0085	0.0153	0.0118
1940	0.0032	0.0081	0.0165	0.0133
1950	0.0034	0.0083	0.0159	0.0125
1960	0.0033	0.0083	0.0181	0.0148
1970	0.0037	0.0105	0.0180	0.0143
Prop 1970	0.0037	0.0091	0.0157	0.0120
$\bar{X}$	0.0037	0.0089	0.0166	0.0131

$LSD_{0.05}$ = 0.0012 g/heat unit across environments within a decade

Table 72. Environment x decade means for rate of dry matter accumulation per heat unit during grain filling (GF) of groups of hybrids selected to represent each decade from 1930 to 1970

Decade of hybrids	Environment: Ames 1981	Ankeny 1981	Ames 1980	Range
	g/heat unit			
1930	0.2061	0.2140	0.1511	0.0629
1940	0.2272	0.2676	0.1618	0.1058
1950	0.2828	0.3092	0.1877	0.1215
1960	0.3032	0.3433	0.1944	0.1489
1970	0.3018	0.3350	0.2060	0.1290
Prop 1970	0.2790	0.3046	0.1991	0.1055
$\bar{X}$	0.2667	0.2953	0.1833	0.1120

$LSD_{0.05}$ = 0.0239 g/heat unit across environments within a decade

Table 73. Means and linear (b_{lin}) and quadratic (b_{quad}) regression coefficients for vegetative dry matter accumulation during grain villing (VEGGF) for four maize hybrids selected to represent each decade at three plant densities

Decade of hybrids	Density			b_{lin}	b_{quad}
	L	M	H		
	VEGGF (g/heat unit)				
1930	-0.0156	-0.0097	-0.0128	-0.0014	-0.0090
1940	0.0145	-0.0146	-0.0207	-0.0176	0.0038
1950	0.0542	0.0123	0.0051	-0.0246	0.0058
1960	0.0636	0.0566	0.0416	-0.0110	0.0013
1970	0.0595	0.0236	-0.0005	-0.0300	0.0020
Prop 1970	0.0598	0.0258	0.0193	-0.0203	0.0046
$LSD_{0.05}$	0.0188	0.0188	0.0188	0.0133	0.0076

per heat unit during all plant growth periods was significant (Table 65). The rate of vegetative dry matter accumulation during grain filling (VEGGF) was negative at Ames 1980, the highest yielding environment.

During all periods of plant growth, except for the seedling stage (VEG1), dry matter accumulation per heat unit was affected by plant density (Table 65). Increasing plant densities reduced the efficiency of the plant to produce dry matter per heat unit. Mutual shading and competition for

other environmental factors by hybrids grown in high plant densities probably were the chief causes of reductions in heat unit efficiency.

Public decade means for all heat unit efficiency traits were significantly different (Table 66). Linear rates of 0.4 ± 0.1, 11.0 ± 1.7, and 24.2 ± 2.0 mg/heat unit/decade for seedling (VEG1), vegetative (VEG2), and grain filling (GF) periods of growth, respectively, best described the change in heat unit efficiency across decades (Tables 66 and 68). VEGGF was negative for the 1930 and 1940 decades, but positive thereafter (Table 66).

Public decade x environment interactions were significant for all heat unit efficiency traits (Table 69). The range among decade means for VEG1 at Ames 1981, the lowest yielding environment, was small, i.e., 0.5 mg/heat unit (Table 71). But, in the highest yielding environment, the 1970 hybrid seedlings produced approximately 2.8 mg dry matter per heat unit more than did their earlier counterparts (Table 71). Hybrids of all decades produced dry matter significantly less efficiently during the grain-filling period in the highest yielding environment, i.e., Ames 1980 (Table 72).

Only VEGGF mean squares for public decades x density interaction were significant (Table 70). Whereas VEGGF for the 1960 decade at high plant density was 0.0416 g/heat unit,

the 1970 hybrids exhibited a loss of -0.0005 g/heat unit at high plant density (Table 73). Linear regression coefficients for VEGGF across plant densities (Table 73) indicated that recent decades of hybrids were not significantly more tolerant of high plant densities in the efficient production of vegetative dry matter during grain filling.

DISCUSSION

The biological basis for machine-harvestable grain yields in maize may be investigated at various levels of complexity. Machine-harvestable grain yields may be viewed simply as the portion of total grain yield that is machine-harvestable as determined by the severity of lodging and dropped ears. A more complete understanding of machine-harvestable grain yields would be achieved, however, if the roles of dry matter production, assimilate partitioning, and sink strength in the production of total grain yield, lodging resistance, and ear retention were understood. Similarly, dry matter production, assimilate partitioning, and sink strength may be characterized by more basic processes, and such an analyses would give a more complex understanding of machine-harvestable grain yields (Figure 26).

Figure 26 is not intended, however, to represent all factors known to contribute to machine-harvestable grain yields, but rather, depicts the hierarchical relationships assumed for the traits measured in this study. These traits were observed in five groups, each consisting of four public hybrids of maize, selected to represent different decades of maize breeding. The decades of maize breeding began with the introduction of hybrid maize in the 1930s and included each successive decade up to the 1970s. Patterns of change in these traits across decades were compared with the pattern of

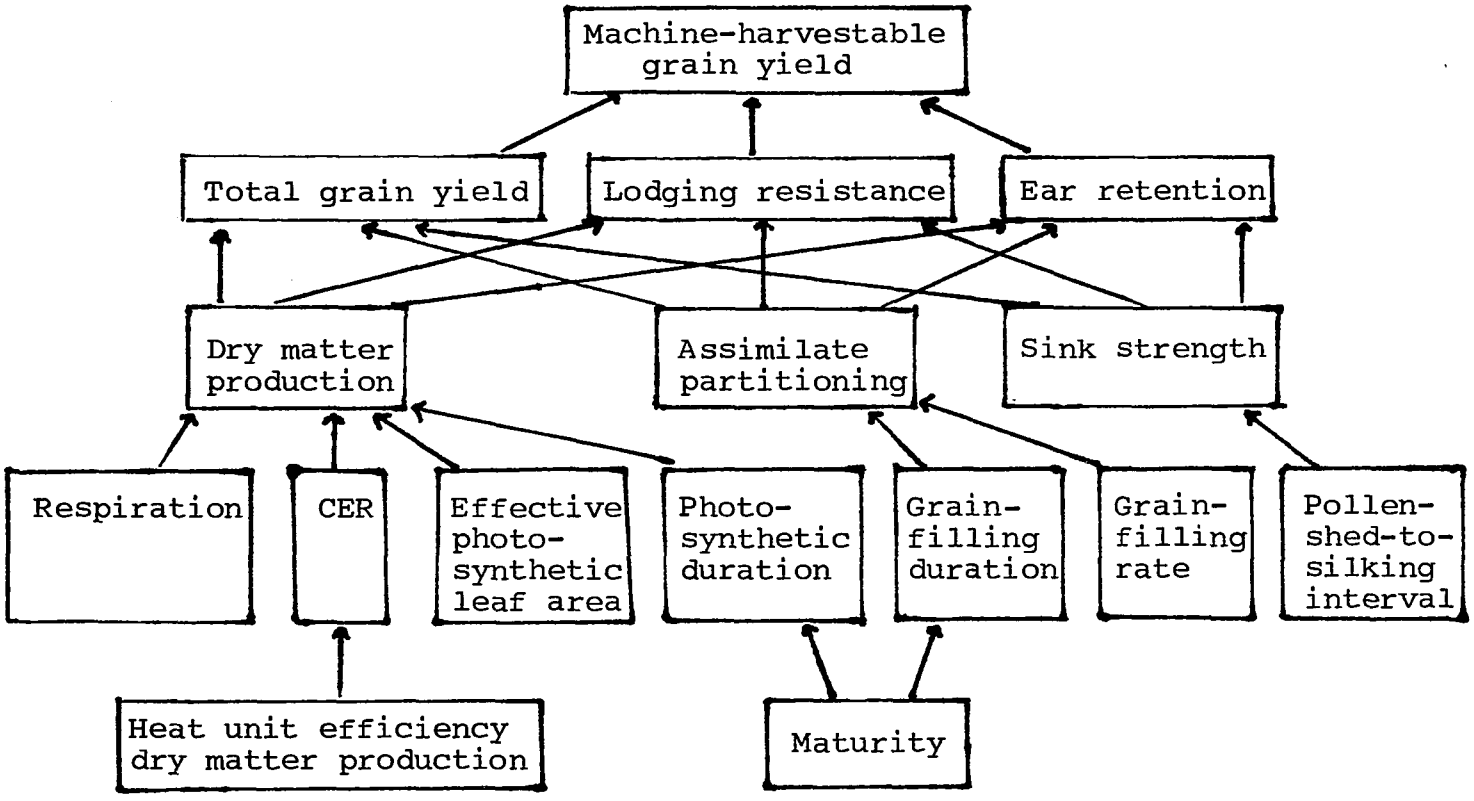

Figure 26. Hierarchical relationships assumed for traits measured in this study

change in machine-harvestable grain yield across decades. Similar patterns of change should indicate some type of an association between that trait and machine-harvestable grain yield and that changes in the trait played a role in the observed changes in machine-harvestable grain yield. Because physiological and morphological traits are closely interrelated in their determination of yield, associations between machine-harvestable grain yield and simpler traits, which contribute less directly to yield, may be obscure. Therefore, to ascertain their contribution to yield, the pattern of change across decades in less complex traits will be compared to that of machine-harvestable grain yield and to those traits to which they contribute more directly (Figure 26). Patterns of change across decades in traits thought to be closely interrelated in the determination of grain yield will be examined in combination. Figure 26 will serve as a format for this discussion.

Harvest Traits

Higher grain yield in association with lodging resistance and ear retention has been the primary goal of maize breeders during the past 40 years. This study demonstrated that machine-harvestable grain yields increased linearly from 47.0 q/ha for the 1930 hybrids to 84.5 q/ha for the 1970 hybrids (Figure 2, Table 7). This represented an increase of 37.5 q/ha or 79.8%. The rate of yield

increase was 0.94 q/ha/year. This rate was considerably greater than 0.62 and 0.50 q/ha/year reported by Russell (1974) and Duvick (1977), respectively.

Figure 26 proposes that increases in machine-harvestable grain yield are due to increases in total grain yield and/or a reduction in lodging and dropped ears. From 1930 to 1970, total grain production increased only 23.4 q/ha (Table 7) compared to an increase of 37.5 q/ha for machine-harvestable grain. The difference between machine-harvestable and total grain yield increases of 14.1 q/ha intuitively appears to be due to improved lodging resistance and ear retention. This indirect indication of improved lodging resistance was substantiated by observed reductions of 27.6 and 10.6% for stalk and root lodging, respectively, between the 1930 and 1970 decades (Table 7). Although machine-harvestable ears increased 31 ears per 100 plants across decades, only 11 of those ears were due to more total ears, indicating that an increase of 20 ears per 100 plants was due to better ear retention and less lodging (Table 49). Although Russell (1974) and Duvick (1977) also reported substantial reductions in stalk and root lodging over the years, they found little change in the number of dropped ears.

The relative contributions of increased total grain yield, improved lodging resistance, and better ear retention to increased machine-harvestable grain yield varied from decade to

decade. Both the linear and cubic regression models mean squares for total grain yield were significant (Table 9). Figure 1 illustrates that significant increases in total grain yield occurred only between the 1930 to 1940 and the 1960 to 1970 decades. Changes in total grain yield between the 1940 and 1960 decades were not statistically or practically significant. Therefore, linear increases in machine-harvestable grain yield between the 1940 and 1960 decades (Figure 2) probably resulted from linear decreases in lodging and increases in machine-harvestable ears (Figures 3, 4, and 18). The increase in machine-harvestable grain yield between the 1960 and 1970 decades, i.e., 10 q/ha, was due entirely to the increase in total grain production as no further reduction in lodging or increases in machine-harvestable ears were observed in this study (Tables 7 and 49). Therefore, the linear pattern of change in machine-harvestable grain yield across decades (Figure 2) was the reflection of the complementation of patterns of change in total grain yield (Figure 1), lodging resistance (Figures 3 and 4), and number of machine-harvestable ears (Figure 18).

Improved maize production practices, e.g., higher plant densities, increased fertilizer applications, more efficient crop management, and better weed control, have made important contributions to increased maize yield. The degree to which maize genotypes are capable of utilizing these improved

production practices to produce higher grain yield may vary. Russell and Balko (1980), for example, reported variation in the efficiency of maize plants to utilize nitrogen fertilizer. Therefore, while modern production practices were applied to all decades of hybrids in this study, they may not have an equal effect on the yield potential of the hybrids representing each decade. This concept is illustrated by Figure 5 which compares machine-harvestable grain yield for each decade of hybrids at low, medium, and high plant densities. The optimum machine-harvestable yield environment for the 1930 and 1940 decades was associated with low plant densities. The 1950 and 1960 decades produced their highest yield at the medium plant density, while high plant densities were required to maximize yields of the 1970 hybrids. Although the potential to produce grain at the low plant density increased 20.2 q/ha since the 1930 decade, the linear increase in machine-harvestable grain at high plant density was 34.7 q/ha (Table 16, Figure 5). Therefore, a portion of the observed linear increase in machine-harvestable grain yield across decades (Figure 2) was related to the use of density-tolerant plants grown at high plant densities.

A density-tolerant plant would have physiological processes and morphological traits enabling it to maintain greater potential performance at high plant densities. Traits displaying increased density tolerance across decades should

give significant public decades x density or public decades linear regression x density interactions in their combined analyses of variance. Studying changes in density tolerance across decades for total grain yield, lodging, and number of machine-harvestable ears per plant should provide a better understanding of the change in density tolerance across decades observed for machine-harvestable grain yield.

Total grain yield, stalk lodging, total ears per plant, and machine-harvestable ears per plant showed significant public decades x density interactions (Tables 11 and 53). As illustrated in Figure 6, the plant density at which greatest total grain yields were produced depended on the decade of hybrids. The linear regression coefficient describing the response of total grain yield to increased plant density (Table 16) indicated a reduction in total grain yield when hybrids of the 1930 decade were grown at higher plant densities. Small increases of 0.7, 6.2, and 5.2 q/ha total grain yield across plant densities were found for the 1940, 1950, and 1960 decades, respectively. The 1970 decade hybrids, however, produced 24.0 q/ha more total grain at the high density than they did at the low plant density. Although linear regression coefficients describing the response of machine-harvestable and total ears per plant to increased plant densities are negative for all decades (Table 58), the magnitude of the negative response was significantly less in the 1960 and 1970

decades of hybrids. Examination of decade by density means for stalk lodging revealed that all significant increases in stalk lodging occurred with the change from low to medium plant densities (Table 16). Increasing plant density from medium to high did not significantly increase stalk lodging. Increases in percentage stalk lodging between the low and medium plant densities for each decade are as follows: 7.0, 1930; 12.0, 1940; 4.6, 1950; 0.8, 1960; 3.4, 1970. Significant improvements in stalk lodging resistance at high plant densities occurred between the 1940 and 1950 decades and the 1950 and 1960 decades (Table 16). The change in density tolerance across decades observed in machine-harvestable grain yields, therefore, was associated with similar changes in density tolerance for total grain production, total and machine-harvestable ears per plant, and stalk lodging resistance.

When studying grain yields per hectare at different plant densities, it is difficult to distinguish the contributions of density tolerance and improved grain yield potential from the contribution of increased plant numbers to total grain yield. Therefore, it is instructive to look at grain yield on a per plant basis. Decade by density means for total grain yield per plant indicated that total grain yield per plant decreased as plant density increased for all decades of hybrids (Table 16). The 1970 maize hybrids, however, produced

33.5 g more grain per plant at the low plant density and 59.0 g grain per plant at the high plant density than did their 1930 counterparts (Table 16). If the low plant density provided the optimum environment for per plant yield, these results suggest that the basic yield potential increased 33.5 g while the remaining 25.5 g of the 59.0 g increase in total grain per plant at high plant density is due to improved density tolerance. A measure of density tolerance can be obtained by expressing total grain at a high plant density as a percentage of the low density total grain yield. Such percentages for each decade are as follows: 46.8, 1930; 51.9, 1940; 54.8, 1950; 54.5, 1960; 63.2, 1970. Distinct increases in density tolerance occurred between the 1930 and 1940 decades and the 1960 and 1970 decades with an apparent plateau between the 1940 and 1960 decades. Similar patterns for density tolerance and total grain yield across decades (Figure 1) provided further evidence that increases in total grain yield across decades were due to both increases in basic yield potential and improved ability to express that yield potential at the high plant density.

The following discussion will consider, first, the physiological and morphological basis for the observed improvements in total grain yield potential, lodging resistance, and number of machine-harvestable ears per plant. Secondly, the contribution of density tolerance in specific traits to

observed density tolerance in more complex traits will be considered. Finally, comparisons of stress tolerance between modern and early hybrids will be made.

Proposed Basis for Increased Machine-Harvestable Maize Grain Yield Potential

Donald and Hamblin (1976) proposed the simple dissection of total grain yield indicated in Figure 26, where total grain yield per plant is the product of dry matter production and the proportion of that dry matter partitioned into the grain, i.e., harvest index. Therefore, the observed increase in total grain yield between the 1930 and 1940 decades (Figure 1) must be due only to increased dry matter production as harvest index was the same for both decades in this study (Tables 24 and 33). Although significant increases in dry matter production occurred between the 1940 and 1950 decades and the 1950 and 1960 decades, they were accompanied by reductions in harvest indices, which resulted in no significant increases in total grain yield during that period (Tables 24 and 33). The observed increase in total grain yield between the 1960 and 1970 decades likely was due, however, to increased partitioning to the grain because no important increase in dry matter production occurred.

Similarly, higher grain yields achieved through increased dry matter production and/or assimilate partitioning to the grain have been reported by Crosbie and Mock (1981). They

indicated that increased grain yield per plant of the improved population BSSS(R) was the result of significantly more assimilate being partitioned to the grain as dry matter per plant had not increased. Higher grain yields of testcrosses of the improved population BSCB1(R) resulted from both increased dry matter production and partitioning to the grain (Crosbie and Mock, 1981). Population crosses of these two improved populations produced more grain, however, in association with increased dry matter production.

Significant increases in machine-harvestable grain yield between the 1940 and 1960 decades were due primarily to improved lodging resistance and number of machine-harvestable ears. Figures 3, 4, and 18 indicate significant reductions in lodging and increases in the number of machine-harvestable ears during that period. These changes allowed a larger portion of the total grain to be machine-harvestable. Between the 1940 and 1960 decades, no significant increases in total grain yield were observed, which indicates no change in the amount of dry matter partitioned to the grain. During that period, however, the maize hybrids produced progressively more dry matter (Figures 10 and 11) which presumably remained in the stalk, ear shank, and roots. Stalks, ear shanks, and roots would be expected, therefore, to be stronger, thus reducing lodging and dropped ears. In this study, patterns of change in dry matter production and assimilate partitioning

complement one another to provide an understanding of the basis of increased total and machine-harvestable grain yield across the decades of maize breeding.

The determinants of net dry matter accumulation evaluated in this study were the rate of photosynthesis per unit leaf area, the amount of effective photosynthetic leaf area, and the duration of the photosynthetic period (Figure 26). In this study, dry matter accumulation increased linearly across decades. The linear pattern of increase was detectable at a seedling stage (Figure 9), 50% silk (Figure 10), and harvest (Figure 11). Decade means for CER were not significantly different (Table 40) and, thus, the increases in dry matter accumulation across decades are likely not due to basic changes in photosynthetic mechanisms. The lack of positive association between CER and dry matter production or grain yield has been reported in several studies (Musgrave, 1971; Crosbie et al., 1978b; Fakorede and Mock, 1978).

The amount of effective photosynthetic area per plant is a function of leaf area and canopy architecture. Mock and Pearce (1975) emphasized the importance of adequate leaf area in association with an erect leaf canopy above the ear in order to maximize interception and penetration of solar radiation. Figures 15 and 16 indicate significant increases in plant leaf area and no change in leaf orientation above the ear between the 1930 and 1950 decades. The 1930, 1940, and

1950 decades of hybrids produced their highest grain yields at low and medium plant densities (Figure 5). At lower plant densities, interception rather than penetration of solar radiation likely is the limitation to efficient use of solar radiation. Observed increases in plant leaf area between the 1930 and 1950 decades may have increased interception of solar radiation at lower plant densities and thus contributed to increased dry matter production. Between the 1950 and 1970 decades, leaf area per plant declined and leaf orientation above the ear became significantly more erect (Figures 15 and 16). The 1960 and 1970 decade hybrids produced their highest total grain yields at the high plant density (Figure 6). At high plant densities, efficient utilization of solar radiation is limited more by penetration of solar radiation into the leaf canopy than by interception of solar radiation. Therefore, more erect leaf canopies of 1960 and 1970 decade hybrids could have contributed to increased effective photosynthetic leaf area at high plant densities and may be associated with observed greater dry matter production. The combination of significant increases in leaf area per plant prior to the 1950 decade and more erect leaf canopies following the 1950 decade suggests that effective photosynthetic leaf area increased across decades. Increases in effective photosynthetic leaf area may be associated with increases in machine-harvestable grain yield by means of its

effect on dry matter production. Earlier studies (Hoyt and Bradfield, 1962; Eik and Hanway, 1966; Williams et al., 1968; Scarsbrook and Doss, 1973; Johnson, 1973; Pendleton et al., 1968; Winter and Ohlrogge, 1973; Lambert and Johnson, 1978; Pepper et al., 1977) have shown a significant relationship between grain yield and both leaf area and leaf orientation.

Total dry matter production is also influenced by duration of the photosynthetic period. Faster germination and establishment of leaf display after planting would lengthen the photosynthetic period at the beginning of the growing season. Spring vigor ratings gave an indication of early photosynthetic potential. An increase in spring vigor ratings across decades (Table 40) indicated that 1970 hybrids displayed more green plant area earlier in the growing season, thus lengthening the duration of the photosynthetic period. Hanson (1971) reported that high dry matter production in juvenile maize plants was associated primarily with 30% greater leaf area. Therefore, an association between more dry matter production and spring vigor in 1970 maize hybrids likely exists. The photosynthetic period also may be lengthened at the end of the growing season by delayed senescence of the plant. Delay of senescence was evaluated by stay green ratings taken just prior to harvest. A linear increase in stay green ratings across decades (Figure 17) with a range of 5 points (1-9 scale) among decade means

(Table 40) indicated a noticeable change in the amount of green leaf area present throughout the grain-filling period. van Eijnatten (1963) and Adelana and Milbourn (1972) have demonstrated an association between increased dry matter production and delay of leaf senescence in certain varieties of maize. Other studies (Duvick, 1977; Fakorede, 1977; Crosbie and Mock, 1981) found increased grain yields to be associated with delayed senescence. Increases in the length of the stay green period across the decades of hybrids likely have contributed directly to increases in dry matter production and indirectly to observed increased total and machine-harvestable grain yields.

Although no estimates of maintenance respiration were made, it is important to recognize its effect on total dry matter accumulation. It is possible that changes in maintenance respiration across decades have influenced accumulated dry matter. Likewise, changes in tassel size could have influenced shading of the upper canopy and dry matter partitioning, but these potential effects were not assessed.

The amount of dry matter partitioned to the grain is a function of the rate of grain filling and the grain-filling duration. Regulation of the rate and duration of grain filling, however, is more obscure. These processes may be limited by sink strength, hormone levels, available assimilate, and other factors.

Figures 12, 13, and 14 reveal no relationship between patterns of change in harvest index and rate of grain filling or grain-filling duration across decades. Harvest indices decreased across decades while duration and rate of grain filling displayed increases of 31.2 heat units and 0.046 mg/heat unit, respectively, between the 1930 and 1970 decades (Tables 33 and 36). Although harvest indices declined, the total amount of dry matter partitioned to the grain has increased across decades (Figure 1). Consequently, the amount of dry matter stored in the grain simply did not increase in proportion to total dry matter. A significant increase in total grain yield between the 1930 and 1940 decades probably was due only to a significantly faster rate of grain filling in the 1940 hybrids as the duration of grain filling did not change. The other significant increase in total grain yield occurred between the 1960 and 1970 decades. This increase in dry matter partitioning to the grain also was due primarily to a significantly faster rate of grain filling because grain-filling duration did not change significantly. Between the 1940 and 1960 decades, no significant increase in total grain yield (Table 7) or rate of grain filling was observed (Table 33). During this period, however, duration of grain filling displayed a significant increase of 34.7 heat units (Table 33). Therefore, these data indicated that increases in total grain yield across decades were

closely associated with increases in the rate of grain filling. Duration of grain filling was not a limitation to the amount of total dry matter partitioned to the grain between the 1930 and 1940 decades and the 1960 and 1970 decades as no significant increase in grain filling duration was associated with observed yield increases. It is possible, however, that the 1970 hybrids used the increases in grain-filling duration which occurred between the 1940 and 1960 decades in combination with a higher rate of grain filling to achieve higher grain yield. Unlike observations made in this study, close associations between grain-filling duration and grain yield have been reported in several studies (Hanway and Russell, 1969; Daynard et al., 1971; Cross, 1975; Fakorede and Mock, 1978; Crosbie and Mock, 1981). The relationship between grain yield and rate of grain filling observed in this study corroborates the work of Crosbie and Mock (1981) who observed significantly higher rates of grain filling in populations of BSSS(R) and BSCB1(R) which had been improved for grain yield. Daynard et al. (1971) and Cross (1975) found no relationship between rate of grain filling and grain yields.

Similar patterns of change across decades were observed for grain-filling duration and stay green ratings (Figures 14 and 17), suggesting that delayed fruit abscission (black layer formation) in maize hybrids was related to delayed senescence

(higher stay green ratings). Although it is not certain whether delayed fruit removal would delay or hasten leaf senescence (Moss, 1962; Allison and Weinmann, 1970), Christensen et al. (1981) recently reported that removal of the maize ear-sink initiated an earlier onset and enhanced rate of senescence.

Mock and Pearce (1975) stressed the importance of adequate sink strength for their maize ideotype. They suggested that maize plants should be prolific so that sink strength would not be a limitation to partitioning of dry matter to the grain. King et al. (1967) and Bingham (1967) have suggested that sink strength may also provide an impetus for dry matter production or exert an effect on assimilate partitioning.

Sink strength for each decade of hybrids was characterized by both kernel size and number. As total grain yield increased across decades (Figure 1), kernel depth and kernel weight also increased, thus generating greater sink strength in later hybrids (Table 49). The cubic pattern of change for kernel number closely paralleled the significant cubic patterns of change in total grain yield per hectare and per plant (Figures 20 and 1 and Table 9). Large increases in kernel number occurred between the 1930 and 1940 decades and the 1960 and 1970 decades with little change between the 1950 and 1960 decades (Table 49). Long kernels, low kernel weight, and high kernel number for the 1940 decade of hybrids (Table

49) suggested a long slender kernel type, unlike the kernel type of other decades, and thus explained the large deviations of the 1940 decade means for kernel weight, length, and number. Therefore, it appears that increases in sink strength have been closely associated with increases in maize yield potential across decades of breeding. Tanaka and Yamaguchi (1972) previously concluded that sink size as determined by number of kernels per unit field area was a limitation to increased grain yields. Significant correlations between sink strength and grain yield also have been reported by El-Lakany and Russell (1971), Obilana and Hallauer (1974), Hallauer (1971), Crosbie et al. (1978a) and Crosbie and Mock (1980). Different sink strength traits were correlated with grain yield in different maize populations, however.

Recall that increased rates of grain filling contributed to observed increases in total dry matter partitioned to the grain and thus to total grain yield increases between the 1930 and 1940 decades and the 1960 and 1970 decades. These increased rates of grain filling likely were very closely associated with the observed increases in kernel number per plant during the same periods of time. Increased rate of grain filling on a per plant basis is more plausible if interpreted as more kernel sinks filling at a normal rate than as the same number of kernels filling at an accelerated rate. Rates of kernel filling for each decade calculated from kernel

weight and duration of grain filling means are as follows: 0.44×10^{-3}, 1930; 0.42×10^{-3}, 1940; 0.43×10^{-3}, 1950; 0.44×10^{-3}, 1960; 0.48×10^{-3}, 1970 g/kernel/heat unit. These rates were not compared statistically, but they appear similar with the exception of the 1970 decade which was slightly higher. Therefore, increases in rate of grain filling for the ear-sink appear to be mostly the result of more kernels per plant and perhaps, in the case of the 1970 decade, also faster rate of kernel filling.

In addition to sink strength, it is also useful to consider the distribution of ear sinks over the crop stand. The total number of plants with ears increased significantly only between the 1930 and 1940 decades (Table 49, Figure 19). The number of plants with machine-harvestable ears, however, increased significantly between all decades except between the 1960 and 1970 decades (Table 49). Therefore, although initiation of ears may not have been a limitation to increased yields after the 1930 decade, the linear increase in the number of plants with ears which were filling grain to physiological maturity has contributed to increased sink strength of the crop stand and to higher grain yield.

A review of the literature suggested that the relationship between yield and plant and/or ear height was unclear (El-Lakany and Russell, 1971; Hallauer, 1971; Vera and Crane, 1970; Acosta and Crane, 1972). In this study, plant height

increased linearly across decades with a significant difference of 18.5 cm between the 1930 and 1970 decades (Table 18). Ear heights for the 1940, 1950, and 1960 decades were significantly lower than the 1930 and 1970 decades which had identical ear heights. The similar patterns of change across decades suggest a relationship between machine-harvestable grain yield and plant height. Moll et al. (1975) proposed the possibility of an optimum ear height for maximum yield. Recognizing the importance of the leaves above the ear, especially those proximal to the ear, in the production of assimilate for the developing grain, they observed that an ear placed on the stalk may result in shading on leaves proximal to the ear and an ear placed high on the stalk may have too few leaves above it. From these observations, it follows that it is the length of stalk above the ear as determined by ear height which is optimum. In this study, the increase in plant height in conjunction with no increase in ear height resulted in an increase in stalk length above the ear across decades of hybrids (Table 18). The effect of an increase in stalk length above the ear on number of leaves and/or the amount of assimilate above the ear was not determined. Therefore, one can only surmise what the effect of increased plant height on grain yield may have been.

Mock and Pearce (1975) pointed out the importance of a short pollen-shed-to-silking interval for their maize ideotype

when grown in high plant densities. Pollen-shed-to-silking intervals exaggerated by high plant densities (El-Lakany and Russell, 1971; Woolley et al., 1962) may result in poor pollinations and barrenness, thus reducing sink strength. The 1970 hybrids displayed a significantly shorter pollen-shed-to-silking interval than all other decades, which were not significantly different from one another (Table 60, Figure 25). The observed decrease between the 1930 and 1970 decades, however, was only 0.7 days. Although the 1970 hybrids did not produce significantly more ears per plant than the 1960 hybrids at high plant density, they did produce significantly more kernels per plant (Table 49). Therefore, a slightly shorter pollen-shed-to-silking interval in the 1970 hybrids may have allowed more pollinations which would contribute to increased kernel number per plant.

Physiological processes and the development of morphological traits are the final expressions of a series of temperature-dependent biochemical processes. Isoenzymes regulating the same chemical process have been shown to have different temperature optima (McNaughton, 1974). It is conceivable, therefore, that different genotypes of maize would be able to germinate, grow, flower, fill the grain, and mature at different rates in a particular growing season characterized by a fixed number of heat units. Differences among decade means for dry matter production per heat unit during all stages of

maize development were significant (Table 66). The change in heat unit efficiency across decades was positive and linear (Table 68). More efficient use of heat units in the production of dry matter during all periods of plant development was closely associated with dry matter production potential in the decades of hybrids.

During the grain-filling period, the 1970 hybrids were able to produce 90.5 mg more dry matter per heat unit than did their 1930 counterparts. Calculations employing observed grain filling durations for the 1930 and 1970 decades (Table 33) indicate that the 1970 hybrids theoretically would produce 72.1 g more dry matter per plant during grain filling than 1930 hybrids. Eastin (1969) reported that 80% of the photosynthate produced during the grain filling period ultimately was translocated to the grain. On this basis, the 1970 hybrids would be expected to produce 57.7 g more grain than 1930 hybrids. This estimate compares favorably with the observed increase of 54.9 g total grain per plant between the 1930 and 1970 decades (Table 7).

Traits Exhibiting Density Tolerance

Although several dry matter related traits displayed significant public decades x density interactions, only dry matter yield means at harvest could be interpreted in terms of density tolerance. Linear positive regression coefficients

for dry matter yield at harvest across plant densities (Table 31) were similar for the 1930, 1940, and 1950 decades but increased significantly for the 1960 and 1970 hybrids. The modern hybrids were able to produce larger amounts of dry matter at the high plant density than were earlier hybrids (Table 31). For example, the 1970 hybrids produced 17.70 mt/ha at high plant density while the 1930 hybrids produced 13.40 mt/ha. However, if harvest dry matter per plant at high plant density was expressed as a percentage of low density dry matter per plant, the following percentages for each decade are generated: 61.1, 1930; 59.2, 1940; 59.6, 1950; 68.1, 1960; 62.6, 1970. These percentages indicated little change in density tolerance for dry matter accumulation per se at harvest across decades. Therefore, while the potential to produce dry matter has increased linearly across decades (Figure 11), the ability to express that potential at high plant densities did not change.

Among the source traits affecting dry matter accumulation, only leaf orientation above the ear (LOVA) and stay green ratings displayed significant public decades x density interactions (Table 44). Although linear regression coefficients describing the change in LOVA across plant densities changed significantly from negative values in the first three decades to positive in the two most recent decades (Table 47), the largest response to an increase in plant density was very

small and presumably not meaningful. Only the 1970 decade linear regression coefficient describing the response of stay green ratings to increased plant density was significantly different from zero (Table 47). The 1970 hybrids had a stay green rating 1.2 points higher at high plant density than they did at the low density (Table 47). This delay of senescence at the high plant density is difficult to understand but may have been associated with observed increases in density tolerance for total grain yield in the 1970 decade hybrids.

The negative linear regression coefficients describing the change in harvest indices across plant densities for the 1930 and 1960 decades are in sharp contrast to the positive responses of the 1950 and 1970 decades (Table 38). The positive responses of the 1950 and 1970 decades indicate a tolerance of high plant density for harvest index. Note, however, that the 1930 decade hybrids partitioned the same percentage of total dry matter to the grain at high plant density as the 1970 decade hybrids. Recall also that the change in density tolerance for machine-harvestable grain yield was linear (Figure 5). Therefore, while certain decades displayed density tolerance for harvest index, the change across decades is not closely associated with the observed change in density tolerance for machine-harvestable grain yield.

Linear regression coefficients describing the effect of increased plant density on grain-filling duration (Table 38)

indicated significant differences in density tolerance between the 1930 and 1970 decades. The decrease in grain-filling duration when grown at high plant density relative to the low density was 31.4 heat units for the 1930 decade and only 7.8 heat units for the 1970 decade (Table 38). The magnitude of the negative responses of rate of grain filling to increased plant density decreased significantly across decades (Table 38). The 1960 and 1970 decades of hybrids displayed greater density tolerance for rate of grain filling. This change in density tolerance for rate of grain filling across decades may be related to the observed changes in density tolerance for kernel number and total grain yield.

Mock (1977) pointed out the limitation on grain yield set by the inability of maize plants to maintain adequate sink strength at high plant densities. For all decades, the number of total and machine-harvestable ears decreased as plant density increased (Table 58, Figures 22 and 23). The magnitudes of these reductions, however, were less in 1960 and 1970 hybrids indicating an increase in density tolerance for ear initiation and ear maintenance on the stalk during the grain-filling period. For example, 1960 and 1970 decade hybrids had a reduction of 14 total ears per 100 plants across plant densities, while the 1930 decade hybrids displayed a reduction of 26 total ears per 100 plants (Table 58). The 1960 and 1970 decade hybrids had 86 machine-harvestable ears per 100

plants at high plant density, whereas the 1930 and 1940 decade hybrids produced only 53 and 66 machine-harvestable ears (Table 58). Maintenance of greater kernel number at high plant densities is closely associated with the observed increase in density tolerance observed for total grain yield in 1970 decade hybrids (Table 58). Likewise, the ability of the 1970 decade hybrids to maintain kernel weight when grown at high plant density was found to be significantly superior to that of the 1930 and 1940 decades (Table 58). In general, increased density tolerance for both machine-harvestable and total grain yield across decades appears to be closely associated with the development of hybrids which are better able to initiate and maintain greater ear-sink strength at high plant density. Crosbie (1978) also found ear-sink strength as determined by ears per plant, kernel depth, and kernels per plant to be correlated with increased grain yield at high plant densities.

Comparisons of Stress Tolerance

The optimum yield environment in this study occurred at Ames in 1980 with a mean total grain yield of 88.3 q/ha and the lowest yield environment occurred at Ames in 1981 with a mean total grain yield of 64.2 q/ha (Table 6). While this study does not provide adequate number or diversity of environments to make a stability analysis, the presence of both

high-yield and low-yield environments allowed cursory comparisons among the decades of hybrids for grain production and certain physiological processes under different levels of environmental stress. Traits for which the decades of hybrids display a differential response to environment would generate significant public decades x environment mean squares in the combined analyses of variance.

The range among environmental means for total grain yield for the 1970 decade, i.e., 18.7 q/ha, is approximately half as large as the comparable range for the 1930 decade, i.e., 35.2 q/ha (Table 12). This indicated that the 1970 hybrids maintained a larger proportion of their yield potential when grown in the low-yield environment than did the 1930 hybrids. Conditions at both Ankeny and Ames in 1981 contributed to increased stalk lodging in all decades (Table 15). Environmental effects were more pronounced, however, on the 1930 and 1940 decade hybrids (Table 15). The 1950, 1960, and 1970 decades of hybrids displayed little variation among environmental means for stalk lodging (Table 15).

Although no differences among decades for dry matter production during the seedling and vegetative stages in the low-yield environment were observed, modern decades of hybrids did make more efficient use of the conditions characterizing the high-yield environment (Tables 29 and 30). The ability to efficiently utilize available environmental

conditions is equally as important to plant stability as the ability to efficiently perform under stress. During the grain-filling period, however, differences in dry matter production per heat unit among the decades were noted in the low-yield environment (Table 72). The 1970 hybrids were more tolerant of the low-yield environment in their production of dry matter per heat unit.

Differences in stress tolerance in the establishment and maintenance of ear-sink strength among decades were noted. The ranges over environments for number of machine-harvestable ears per 100 plants were 33 and 7 for the 1930 and 1970 decades, respectively (Table 57). Clearly, the modern hybrids are more tolerant of stress in the establishment and maintenance of machine-harvestable ears. Note that the greatest improvements in stress tolerance for machine-harvestable and total ears per plant, kernel depth, and kernel number occurred, however, between the 1930 and 1940 decades (Tables 54-57).

Public versus Proprietary Maize Hybrids for the 1970 Decade

In general, the 1970 public maize hybrids' performance was superior to that of the 1970 proprietary hybrids. The public hybrids produced 9.3 q/ha more machine-harvestable grain and 10.5 q/ha more total grain than the proprietary hybrids (Table 7). These differences were statistically

significant. Lodging and number of machine-harvestable ears per plant did not differ significantly between the public and proprietary hybrids (Tables 7 and 49).

The 1970 public hybrids accumulated significantly more dry matter at all stages of plant development than did the proprietary hybrids (Table 24). The proprietary hybrids displayed a significantly higher rate of carbon dioxide exchange than did the public hybrids (Table 40), but this trait was apparently not associated with differences in dry matter production. The only other source traits for which the public and proprietary hybrids differed significantly were leaf orientation above the ear and spring vigor rating (Table 40). The greater dry matter production of the public hybrids may have resulted in part from a more erect leaf canopy and/or greater leaf display early in the growing season.

Although harvest indices displayed by the public and proprietary hybrids were not significantly different (Table 33), public hybrids partitioned more dry matter to the grain (Table 7). The duration of grain filling was significantly longer, i.e., 28.7 heat units, in the proprietary hybrids (Table 33) than in the public hybrids. However, it appeared that the significantly faster rate of grain filling in the public hybrids (Table 33) was more closely related to total dry matter partitioned to the grain than was grain-filling duration.

The ear-sink of the public hybrids was significantly larger than the ear-sink of the proprietary hybrids. The public hybrids produced 62.0 more kernels per plant than did the proprietary hybrids (Table 49). The kernels of the public hybrids weighed 0.03 g more than the kernels of the proprietary hybrids (Table 49). The faster rate of grain filling in the public hybrids was likely associated with their greater kernel number.

The proprietary hybrids flowered a significant 27.2 heat units earlier than did the public hybrids (Table 60). The practical importance of this difference is difficult to assess.

Therefore, differences in grain yield between the 1970 public and proprietary hybrids were most closely associated with differences in dry matter production and kernel number per plant.

Maize Breeder Recommendations

Based on the results of this study, recommendations to maize breeders may be made. First, evaluation of maize populations, synthetics and inbreds for morphological and physiological traits which are related to grain yield would allow breeders to select parental materials which complement one another. Populations developed from crosses of selected populations or inbreds may be used in recurrent selection

programs and development of inbred lines or the maize ideotype. Incorporation of traits by backcrossing methods may improve populations and inbred lines.

Secondly, selection for desirable traits which were present in the parental materials should continue wherever possible in association with yield testing in recurrent selection and line development schemes. The results of this study indicated that high grain yield potential was associated primarily with ear-sink strength and dry matter production. Heritabilities for morphological and physiological traits associated with ear-sink strength and dry matter production often are not high. Selection among and within lines for desirable physiological and morphological traits, as well as agronomic traits, however, can be done in most breeding programs. This may provide a means of eliminating plants with less genetic potential. Selection for physiological and morphological traits can be continued throughout inbreeding. The absence of the desired traits in lines would allow their elimination prior to yield testing. Selection among the best lines whose grain yields did not differ may be based on the physiological and morphological traits they display.

Evaluation of many traits found to be associated with ear-sink strength and dry matter production could easily be incorporated into most breeding programs. Dry matter production was associated with better spring vigor, higher stay

green ratings, adequate leaf area, and an erect leaf orientation. Visual assessment of these traits should be made to maintain the effective canopy structure of modern hybrids and to increase the photosynthetic period. Stay green ratings should be made only on plants with ears and comparisons made only among maize lines of similar maturity. Ear-sink strength was associated with barrenness at high plant density and kernel weight, depth and number. Maize lines should be grown at plant densities which promote barrenness and those lines with short pollen-shed-to-silking intervals and more machine-harvestable ears should be selected. At harvest, kernel rows, number, depth, and weight should be determined and used in association with yield test data to select the superior lines. Selection for these traits within lines will not be as effective as it is among lines but, nevertheless, should be employed. Although more cumbersome to evaluate, dry matter per plant at harvest would provide another means of selecting among the highest yielding lines.

Finally, this study has suggested many questions which the breeder may investigate to expand his understanding of the basis of maize grain yield. How did the modern hybrids accumulate more dry matter? Why did modern hybrids produce more kernels per plant? Is there a relationship between senescence and kernel abscision? These are a few of the questions which need to be investigated.

SUMMARY AND CONCLUSIONS

Four single-cross maize hybrids were selected to represent the germplasm used during each decade from the 1930s to the 1970s. These hybrids were grown at low, medium, and high plant densities in four environments (Agronomy and Agricultural Engineering Research Center, near Ames, Iowa in 1980 and 1981; Ankeny Research Center, near Ankeny, Iowa in 1980 and 1981). A split-plot design was used. Plant densities were main plots and hybrids were subplots. My objectives were (1) to evaluate changes in machine-harvestable and total grain yield across decades of maize breeding, (2) to study changes in the "source" of assimilate that were related to increased grain yield potential, (3) to examine the relationship between changes in the ear-sink and in grain yield potential, (4) to determine the relationship between changes in the partitioning of assimilate and in grain yield potential, and (5) to compare the performance of decades of hybrids at low, medium, and high plant densities.

This study demonstrated that machine-harvestable grain yields increased linearly from 47.0 q/ha for the 1930 hybrids to 84.5 q/ha for the 1970 hybrids. From 1930 to 1970, total grain production increased only 23.4 q/ha compared to an increase of 37.5 q/ha for machine-harvestable grain. Improved lodging resistance and ear retention contributed 14.1 q/ha to observed increases in machine-harvestable grain yield

across decades. Stalk and root lodging decreased 27.6 and 10.6%, respectively, between the 1930 and 1970 decades. Machine-harvestable ears increased 31 ears per 100 plants across decades, but only 11 of those ears were due to more total ears. Significant increases in total grain yield occurred only between the 1930 and 1940 decades and the 1960 and 1970 decades. The pattern of change in total grain yield across decades was cubic. Therefore, the linear pattern of change in machine-harvestable grain yield across decades was the reflection of the complementary patterns of change in total grain yield, lodging resistance, and number of machine-harvestable ears.

A portion of the observed linear increase in machine-harvestable grain yield across decades was related to the use of density-tolerant plants grown at higher plant densities. The change in density tolerance across decades observed in machine-harvestable grain yields was associated with similar changes in density tolerance for total grain production, total and machine-harvestable ears plant, and stalk lodging resistance.

The potential of the hybrids as a source of assimilate increased linearly across decades. The linear pattern of increase was detectable at a seedling stage, 50% silk, and harvest. Significant increases in dry matter production across decades were not due to faster rates of carbon dioxide

exchange (CER) because changes in CER across decades were nonsignificant. The combination of significant increases in leaf area per plant prior to the 1950 decade and more erect leaf canopies following the 1950 decade suggested that effective photosynthetic leaf area increased across decades and may have been associated with increases in dry matter production and machine-harvestable grain yield. The duration of the photosynthetic period increased across decades due to significant delays in leaf senescence. Increases in the length of the stay green period likely have contributed directly to increases in dry matter production and indirectly to observed increased total and machine-harvestable grain yield.

The total amount of dry matter partitioned to the grain increased significantly between the 1930 and 1940 decades and the 1960 and 1970 decades. The increases in total grain yield probably were due to significantly faster rates of grain filling because grain-filling duration did not change during these time periods. Harvest index did not change between the 1930 and 1940 decades, decreased between the 1940 and 1960 decades, but increased between the 1960 and 1970 decades. The decreases in lodging resistance between the 1940 and 1960 decades were associated with the increases in dry matter production accompanied by reductions in harvest index.

Ear-sink strength for each decade of hybrids was characterized by both kernel size and kernel number. Kernel depth and kernel weight increased across decades. The pattern of change in kernel number was cubic. Therefore, kernel number appeared to be closely associated with rate of grain filling and total grain yield which displayed similar patterns of change. The number of plants with machine-harvestable ears increased significantly between all decades except between the 1960 and 1970 decades, and was associated with increases in machine-harvestable grain.

The 1970 hybrids displayed a significantly shorter pollen-shed-to-silking interval than all other decades. The other intervals were not significantly different from one another. The observed decrease was only 0.7 days and likely was associated with the observed increase in kernel number in the 1970 hybrids.

Increased density tolerance for both machine-harvestable and total grain yield across decades appeared to be closely associated with the development of hybrids which are better able to initiate and maintain greater ear-sink strength at high plant density. Modern hybrids displayed density tolerance for total and machine-harvestable ears, kernel number, and kernel weight.

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APPENDIX

Table A1. Degrees of freedom for traits not measured in all environments

Source of variation	Trait									
	Emergence	Seedling dry wt.		Dry wt. at 50% silk		CER	Rating		Plts. with tillers	HI
		PP[a]	Y[a]	PP	Y		Spr. vig.	Stay gr.		
Environment (E)	2	2	2	2	2	1	3	2	3	3
Reps/E	6	6	6	6	6	4	8	6	8	7
Density (D)	2	2	2	2	2	2	2	2	2	2
D x E	4	4	4	4	4	2	6	4	6	6
Error a	12	12	12	12	12	8	16	12	16	14
Hybrid (H)	23	23	23	23	23	23	23	23	23	23
H x E	46	46	46	46	46	46	69	46	69	69
H x D	46	46	46	46	46	46	46	46	46	46
H x D x E	92	92	92	92	92	46	138	92	138	138
Error b	414	414	414	413	413	268	552	414	551	478
H x E	46	46	46	46	46	46	69	46	69	69
Decades x E	10	10	10	10	10	10	15	10	15	15
Public decades x E	8	8	8	8	8	8	12	8	12	12
Linear x E	2	2	2	2	2	2	3	2	3	3
Quadratic x E	2	2	2	2	2	2	3	2	3	3
Cubic x E	2	2	2	2	2	2	3	2	3	3
Lack of fit x E	2	2	2	2	2	2	3	2	3	3
1970 vs Prop 1970 x E	2	2	2	2	2	2	3	2	3	3

[a]PP, per plant; Y, yield.

Table A1. (Continued)

Source of variation	Trait									
	Emergence	Seedling dry wt.		Dry wt. at 50% silk		CER	Rating		Plots. with tillers	HI
		PP	Y	PP	Y		Spr. vig.	Stay gr.		
H/decades x E	36	36	36	36	36	36	54	36	54	54
1930 x E	6	6	6	6	6	6	9	6	9	9
1940 x E	6	6	6	6	6	6	9	6	9	9
1950 x E	6	6	6	6	6	6	9	6	9	9
1960 x E	6	6	6	6	6	6	9	6	9	9
1970 x E	6	6	6	6	6	6	9	6	9	9
Prop 1970 x E	6	6	6	6	6	6	9	6	9	9

Table A2. Means for harvest traits of maize hybrids grown at three plant densities in four environments

Hybrids	Grain yield		Grain yield/plant		Percent lodging		Grain moisture
	Total	Harvestable	Total	Harvestable	Root	Stalk	
	(q/ha)		(g)		(%)		(%)
Os420xL289	68.74	43.75	172.0	111.7	14.5	58.3	16.6
Os420xI205	71.53	56.12	177.6	143.1	2.7	8.4	19.7
L289xI205	69.80	60.54	175.5	154.8	8.1	29.1	17.4
Os426xC144&	47.79	27.76	115.9	65.1	42.5	38.8	16.4
Wf9xOs420	70.71	56.35	184.1	151.2	5.2	14.2	17.2
M14xL87-2	71.61	62.60	180.0	161.1	10.2	20.8	17.2
I205x187-2	78.81	68.52	193.2	169.7	9.2	19.4	18.3
M14xL289	74.18	59.24	184.5	150.5	10.8	38.7	17.8
B14AxWf9	79.12	74.53	195.4	185.7	1.4	3.4	16.8
M14xB14A	70.69	68.37	170.3	165.8	0.8	5.2	17.3
187-2xB14A	74.47	70.66	187.1	179.6	6.6	11.0	17.1
Wf9x187-2	75.20	69.68	188.7	177.0	21.3	14.5	17.0
B14AB54	77.57	76.46	190.4	188.3	7.4	1.1	18.4
B37xB54	77.25	75.95	193.7	191.3	12.1	6.0	18.7
Oh43xB37	77.00	76.64	189.7	189.0	1.4	3.4	19.6
Oh43xB14A	69.92	68.85	180.3	178.2	2.3	4.2	18.6
B73xMo17	90.48	85.72	219.4	208.2	3.6	2.4	18.6
B73xB70	95.83	92.71	232.0	225.9	6.0	8.2	21.0
B37xB70	92.55	89.70	224.8	219.5	13.7	9.7	18.9
A632xMo17	72.55	69.69	181.8	176.1	2.2	3.8	16.2
DeKalb XL55a	76.02	75.62	182.5	181.5	0.8	9.4	17.4
Pioneer 3541	74.23	71.66	182.0	176.8	0.0	0.6	16.2
Northrup Px37	71.82	67.26	173.3	163.4	1.5	3.1	15.8
Funks 4520	87.42	86.29	212.0	209.9	5.1	1.6	19.1
$LSD_{0.05}$	10.78	14.76	26.06	29.38	11.0	17.0	0.9

Table A3. Means for plant traits of maize hybrids grown at three plant densities in four environments[a]

Hybrids	Plant height (cm)	Ear height (cm)	Emergence (%)
Os420xL289	211.7	118.6	92.0
Os420xI205	201.7	103.8	84.7
L289xI205	214.3	120.5	87.3
Os426xC1447	204.5	127.0	89.5
Wf9xOs420	214.7	104.6	87.7
M14xL87-2	192.5	102.4	96.2
I205x187-2	206.4	119.5	85.7
M14xL289	213.6	119.3	94.6
B14AxWf9	214.7	117.6	89.7
M14xB14A	199.8	99.5	92.0
187-2xB14A	211.3	117.8	89.1
Wf9x187-2	218.8	120.7	92.7
B14AxB54	232.8	125.0	88.0
B37xB54	237.6	122.8	86.7
Oh43xB37	208.5	100.3	93.8
Oh43xB14A	216.4	105.6	91.6
B73xMo17	221.3	122.5	96.1
B73xB70	227.0	120.5	94.3
B37xB70	219.5	117.7	90.0
A632xMo17	218.0	109.5	94.0
DeKalb XL55a	218.5	110.5	87.9
Pioneer 3541	204.8	99.8	93.8
Northrup Px37	202.7	101.8	94.2
Funks 4520	218.8	112.2	90.2
$LSD_{0.05}$	7.4	5.4	5.2

[a]Emergence was determined in three environments.

Table A4. Means for dry matter accumulation traits of maize hybrids grown at three plant densities in several environments

Hybrids	Seedling dry weight		Dry weight at 50% silk		Dry weight at harvest		Veg. DM per plant at harvest (g)	HI grain wt./ plant (g)
	Per plant (g)	Yield (kg/ha)	Per plant (g)	Yield (mt/ha)	Per plant (g)	Yield (mt/ha)		
Os420xL289	4.12	379.9	155.4	6.30	309.6	12.28	139.4	170.2
Ox420xI205	2.93	242.5	140.4	5.81	326.6	13.60	151.6	175.0
L289xI205	3.16	261.9	139.4	5.81	299.5	12.47	127.4	172.1
Os426xC1447	3.47	309.1	160.6	6.49	259.8	11.10	139.6	120.2
Wf9xOs420	3.82	342.3	168.9	6.84	347.2	14.16	170.4	176.8
M14x187-2	3.51	343.7	157.3	6.52	332.9	13.67	159.0	173.9
I205x187-2	3.07	257.2	145.4	5.99	321.0	12.77	140.4	180.6
M14xL289	3.62	342.5	164.4	6.73	329.5	13.44	160.0	169.5
B14AxWf9	3.29	293.5	172.6	7.06	396.3	15.96	211.8	183.1
M14AxB14A	3.67	333.2	158.9	6.47	343.8	13.76	178.0	165.9
187-2xB14A	3.52	314.5	168.3	6.74	368.3	14.86	191.3	177.0
Wf9x187-2	3.35	314.9	166.7	6.74	363.9	14.74	178.5	184.4
B14AxB54	4.44	386.8	177.2	7.30	399.3	16.49	218.1	181.2
B37xB54	4.28	387.4	176.1	7.15	395.2	16.16	218.9	176.4
Oh43xB37	3.46	318.9	162.9	6.70	385.3	16.18	318.1	167.2
Oh43xB14A	3.13	285.3	174.0	6.91	372.8	15.16	208.9	163.9
B73xMo17	3.84	373.1	181.6	7.45	400.7	16.43	195.0	205.8
B73xB70	4.26	400.0	182.6	7.53	403.5	16.37	207.7	195.8
B37xB70	4.00	360.1	177.5	7.46	403.0	16.84	208.8	194.3
A632xMo17	4.02	384.2	172.4	7.17	369.5	15.04	186.9	182.6
DeKalb XL55a	4.27	376.6	155.1	6.41	363.1	15.13	192.6	170.6
Pioneer 3541	3.35	313.4	148.2	6.35	356.7	15.33	179.5	177.2
Northrup Px37	3.39	324.5	153.3	6.50	350.9	14.66	169.6	181.3
Funks 4520	3.22	290.9	157.1	6.38	380.4	15.41	190.1	190.3
$LSD_{0.05}$	0.82	72.2	16.6	0.64	25.4	1.54	19.6	16.0

Table A5. Means for assimilate partitioning traits of maize hybrids grown at three plant densities in several environments

Hybrids	HI (%)	Rate of grain filling		Grain filling duration	
		g/heat unit	g/ day	heat units	days
Os420xL289	53.8	0.2802	3.27	662.9	56.8
Os420xI205	53.0	0.2877	3.09	747.7	66.6
L289xI205	57.4	0.2837	3.18	713.3	62.5
Os426xC1447	46.4	0.2146	2.35	675.3	57.6
Wf9xOs420	50.4	0.3003	3.33	703.9	63.1
M14x187-2	52.1	0.2671	3.12	710.5	63.3
I205x187-2	56.6	0.2827	3.35	697.4	62.1
M14xL289	51.8	0.2961	3.35	685.1	59.3
B14AxWf9	47.0	0.2791	2.99	753.3	70.0
M14xB14A	48.7	0.2507	2.69	756.7	69.3
187-2xB14A	48.4	0.2692	2.91	732.9	68.3
Wf9x187-2	50.8	0.2783	3.14	730.1	67.3
B14AxB54	44.1	0.2861	3.08	745.6	67.3
B37xB54	44.5	0.2939	3.46	711.1	63.1
Oh43xB37	43.8	0.2659	3.11	735.7	64.9
Os43xB14A	43.7	0.2909	2.95	743.2	67.3
B73xMo17	51.4	0.3239	3.46	749.8	70.0
B73xB70	48.8	0.3162	3.61	747.4	67.9
B37xB70	48.5	0.3251	3.77	702.2	62.4
A632xMo17	50.1	0.2821	3.14	724.7	64.6
DeKalb XL55a	47.3	0.2610	3.04	744.8	65.5
Pioneer 3541	49.9	0.2557	2.84	795.0	72.1
Northrup Px37	51.0	0.2705	2.94	731.7	63.6
Funks 4520	50.0	0.2958	3.24	767.4	70.8
$LSD_{0.05}$	3.6	0.0358	0.46	23.9	2.5

Table A6. Means for source traits of maize hybrids grown at three plant densities in several environments[a]

Hybrids	CER	PLA	LAI	LOVA	LOVB	Spring vigor rating	Stay green rating	Plants with tillers (%)
Os420xL289	42.0	70.0	2.9	27.8	31.6	7.1	1.1	3.6
Os420xI205	38.3	67.2	3.0	31.1	32.0	6.5	2.6	8.9
L289xI205	41.7	66.4	2.9	27.4	29.7	6.7	2.7	3.7
Os426xC1447	38.3	69.2	3.2	22.9	27.7	5.8	1.0	84.2
Wf9xOs420	37.4	73.1	3.1	26.3	29.6	7.0	2.3	4.5
M14x187-2	37.8	68.8	3.0	24.6	26.0	5.9	2.6	6.2
I205x187-2	38.9	66.3	2.8	27.1	28.6	6.2	3.3	5.4
M14xL289	41.1	78.5	3.4	27.7	28.6	6.6	2.6	3.6
B14AxWf9	39.9	79.4	3.4	23.9	28.7	6.7	5.6	4.2
M14xB14A	44.0	78.4	3.3	20.3	24.4	6.1	4.9	7.4
187-2xB14A	40.2	73.9	3.1	31.0	30.3	6.5	4.6	5.0
Wf9x187-2	35.4	70.7	3.0	27.6	29.5	6.6	4.1	3.2
B14AxB54	39.7	70.1	3.0	29.8	32.0	7.0	6.4	3.2
B37xB54	38.6	68.3	2.9	29.6	32.3	7.1	6.7	2.8
Oh43xB37	38.8	68.2	2.9	33.8	34.4	6.3	7.3	3.3
Oh43xB14A	45.0	75.0	3.2	28.2	31.8	6.0	6.6	11.3
B73xMo17	37.6	70.4	3.0	56.6	34.8	6.9	3.6	2.0
B73xB70	37.4	72.9	3.1	42.7	31.5	7.0	3.6	4.0
B37xB70	32.9	70.3	3.0	41.2	31.6	7.3	5.8	2.2
A632xMo17	40.3	71.2	3.0	31.6	30.8	7.0	4.6	3.8
DeKalb XL55a	41.3	71.8	3.2	36.2	30.6	7.4	4.4	3.8
Pioneer 3541	41.1	66.0	2.9	40.7	35.0	6.2	5.0	7.1
Northrup Px37	40.0	66.7	2.9	32.9	29.6	6.6	4.0	3.2
Funks 4520	42.0	71.2	3.0	42.8	33.7	6.3	5.3	4.2
$LSD_{0.05}$	6.8	5.4	0.38	3.4	2.2	0.4	1.8	14.8

[a]See footnote a, Table 39, page 111.

Table A7. Means for ear-sink traits of maize hybrids grown at three plant densities in four environments

Hybrids	Ear length (cm)	Kernel depth (mm)	Kernel weight (g)	Kernel number/ plant	Total ears/ plant	Harvestable ears/ plant
Os420xL289	19.9	9.2	0.327	529.3	0.86	0.60
Os420xI205	17.6	10.3	0.309	569.8	0.84	0.65
L289xI205	19.4	9.2	0.306	578.5	0.88	0.79
Os426xC1447	16.6	7.3	0.281	413.1	0.77	0.48
Wf9xOs420	18.2	10.6	0.333	558.0	0.86	0.70
M14x187-2	20.3	9.3	0.265	675.2	0.95	0.83
I205x187-2	19.2	9.8	0.282	685.5	0.93	0.82
M14xL289	20.3	9.9	0.289	640.4	0.99	0.82
B14AxWf9	21.1	10.0	0.331	589.5	0.94	0.91
M14xB14A	20.2	9.2	0.333	510.4	0.97	0.95
187-2xB14A	20.8	9.0	0.328	572.6	0.92	0.88
Wf9x187-2	19.8	9.8	0.301	624.4	0.88	0.82
B14AxB54	20.0	9.8	0.371	514.4	0.92	0.91
B37xB54	18.8	10.2	0.340	562.6	0.96	0.94
Oh43xB37	19.4	9.7	0.282	665.2	0.96	0.95
Oh43xB14A	21.0	9.2	0.308	579.7	0.94	0.93
B73xMo17	20.3	10.1	0.330	667.8	0.96	0.93
B73xB70	18.3	10.3	0.408	713.6	1.00	0.98
B37xB70	19.4	10.3	0.324	689.0	1.00	0.97
A632xMo17	20.0	9.3	0.353	515.9	0.93	0.90
DeKalb XL55a	19.4	9.7	0.334	546.4	0.98	0.97
Pioneer 3541	17.5	10.4	0.309	589.8	0.96	0.94
Northrup Px37	20.7	9.2	0.353	490.0	0.91	0.88
Funks 4520	18.8	10.3	0.300	712.2	0.97	0.96
$LSD_{0.05}$	1.0	0.7	0.052	87.0	0.10	0.06

Table A8. Means for flowering traits of maize hybrids grown at three plant densities in four environments

Hybrids	Pollen shed			Silk extrusion			Interval[a]			Heat units at 50% silk
	25%	50%	75%	25%	50%	75%	Silking	PS	PS to silk	
	(days after July 1)						(days)			
Os420xL289	12.2	12.9	14.3	14.8	16.7	19.3	4.6	2.1	3.8	856.8
Ox420xI205	13.2	14.3	16.0	15.2	17.2	19.7	4.5	2.8	2.8	862.2
L289xI205	13.1	14.3	16.3	15.0	16.9	20.0	5.0	3.2	2.6	858.7
Os426xC1447	12.9	14.1	15.5	15.6	17.4	19.8	4.2	2.6	3.3	866.2
Wf9xOs420	12.4	13.6	15.4	17.1	18.8	22.2	5.1	3.0	5.2	886.1
M14x187-2	15.4	16.8	18.2	17.6	19.0	20.7	3.1	2.8	2.2	890.5
I205x187-2	15.3	16.6	18.4	17.1	18.6	21.6	4.4	3.1	2.0	883.9
M14xL289	13.8	15.2	17.1	16.5	18.1	20.7	4.2	3.2	2.9	878.2
B14AxWf9	15.1	16.3	18.1	18.6	20.3	22.3	3.8	3.0	4.1	904.7
M14xB14A	15.7	16.8	18.5	17.9	19.8	21.8	3.9	2.7	3.1	902.4
187-2xB14A	16.9	18.2	20.1	19.2	21.0	23.4	4.3	3.2	2.9	915.9
Wf9x187-2	15.9	17.3	18.8	18.8	20.4	22.5	3.7	2.8	3.2	908.2
B14AxB54	15.6	16.9	18.7	18.3	19.8	22.5	4.3	3.2	3.0	901.2
B37xB54	14.4	15.6	17.1	16.4	17.9	20.3	3.9	2.7	2.3	871.3
Os43xB37	14.0	15.3	16.9	16.5	18.0	20.3	4.0	2.9	2.9	874.3
Os43xB14A	15.4	16.6	18.2	18.2	20.3	23.1	4.9	2.8	3.6	904.6
B73xMo17	15.9	17.2	19.3	18.9	20.3	22.6	3.7	3.3	3.1	907.2
B73xB70	15.9	17.1	18.8	17.1	18.7	20.8	3.6	2.8	1.7	884.7
B37xB70	15.3	16.6	18.3	16.9	18.5	21.1	4.1	2.9	1.9	882.7
A632xMo17	13.9	15.1	16.3	15.8	17.5	19.8	4.0	2.7	2.7	866.5
DeKalb XL55a	13.9	15.1	16.9	14.4	15.8	18.2	3.8	2.9	0.8	844.8
Pioneer 3541	13.3	14.4	15.8	14.6	16.5	18.7	4.1	2.6	2.1	854.5
Northrup Px37	14.1	15.3	16.9	15.0	16.6	19.1	4.1	2.8	1.4	854.7
Funks 4520	14.3	15.6	17.5	16.8	18.3	20.6	3.7	3.2	2.8	878.3
$LSD_{0.05}$	1.0	1.2	1.4	0.8	1.0	1.6	1.2	0.6	1.2	14.1

[a]PS, pollen shed.

Table A9. Means for heat unit efficiency traits of maize hybrids grown at three plant densities in three environments

Hybrids	VEG1	VEG2	VEG3	GF	VEGGF
	(g/heat unit)				
Os420xL289	0.0110	0.2916	0.1790	0.1906	-0.0220
Os420xI205	0.0078	0.2634	0.1607	0.2419	0.0147
L289xI206	0.0084	0.2621	0.1601	0.1966	-0.0196
Os426xC1447	0.0092	0.2981	0.1829	0.1326	-0.0238
Wf9xOs420	0.0102	0.3022	0.1888	0.2187	-0.0059
M14x187-2	0.0092	0.2823	0.1752	0.2269	0.0023
I205x187-2	0.0081	0.2614	0.1623	0.2161	-0.0155
M14xL289	0.0096	0.3022	0.1854	0.2139	-0.0087
B14AxWf9	0.0089	0.2990	0.1882	0.2832	0.0429
M14xB14A	0.0096	0.2813	0.1760	0.2321	0.0125
187-2xB14A	0.0093	0.2904	0.1831	0.2658	0.0273
Wf9x187-2	0.0089	0.2907	0.1822	0.2604	0.0124
B14AxB54	0.0118	0.3126	0.1962	0.2800	0.0451
B37xB54	0.0112	0.3187	0.1980	0.2924	0.0563
Oh43xB37	0.0091	0.2984	0.1830	0.2820	0.0641
Oh43xB14A	0.0082	0.3045	0.1899	0.2673	0.0504
B73xMo17	0.0102	0.3187	0.o989	0.2910	0.0187
B73xB70	0.0113	0.3324	0.2052	0.2934	0.9354
B37xB70	0.0110	0.3205	0.1988	0.2910	0.0403
A632xMo17	0.0108	0.3199	0.1961	0.2483	0.0157
DeKalb XL55a	0.0114	0.2980	0.1804	0.2612	0.0456
Pioneer 3541	0.0089	0.2851	0.1716	0.2550	0.0362
Northrup Px37	0.0091	0.2901	0.1762	0.2454	0.0219
Funks 4520	0.0086	0.2843	0.1762	0.2821	0.0362
$LSD_{0.05}$	0.0020	0.0314	0.0181	0.0338	0.0380